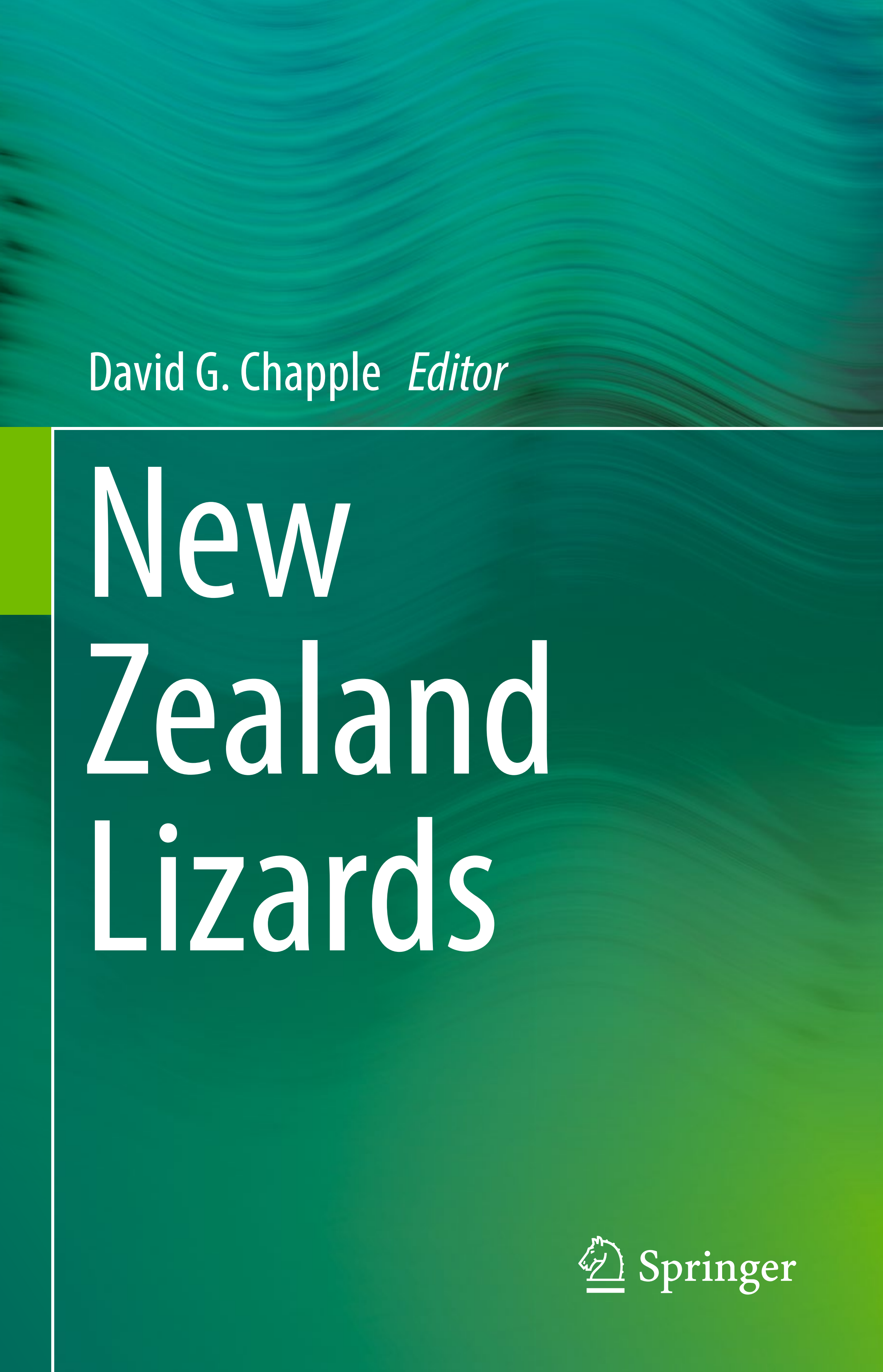


David G. Chapple *Editor*

New Zealand Lizards

Springer

New Zealand Lizards

David G. Chapple
Editor

New Zealand Lizards

Springer

Editor
David G. Chapple
School of Biological Sciences
Monash University
Clayton, Victoria
Australia

ISBN 978-3-319-41672-4 ISBN 978-3-319-41674-8 (eBook)
DOI 10.1007/978-3-319-41674-8

Library of Congress Control Number: 2016953846

Printed on acid-free paper

This Springer imprint is published by Springer Nature
The registered company is Springer International Publishing AG Switzerland

For Kira and Nicole

Foreword

Like many young Australians of my generation, my first trip overseas was to New Zealand, when I was 20 years of age. But unlike most of my compatriots, my journey was driven by my fondness for reptiles. I was invited to join a scientific expedition to Stephens Island, in the middle of Cook Strait, to study the almost-mythical Tuatara. I was entranced by these large dragon-like creatures—spectacular survivors of a once-mighty evolutionary lineage, clinging to existence on the rocky shores of a few windswept islands. In my undergraduate lectures, I had heard all about the lordly Tuatara, as well as the desperately endangered Stephens Island Frog. But I was astonished when, halfway through the trip, I found a small, elegantly striped gecko. Until then, I was blissfully unaware of the lizards of New Zealand. Distracted by the few living survivors of archaic groups, I had forgotten—or more likely, never realised—that New Zealand is also home to a spectacular evolutionary radiation of lizards.

My ignorance reflected a widespread phenomenon: until recently, the lizards of New Zealand were the epitome of a neglected group. Neglected by science, neglected by the public, and neglected by wildlife managers. Despite their astonishing diversity—we now know there are more than 100 species—the New Zealand lizards for long lived in the shadow of the Tuatara, their more famous reptilian relative. Thankfully, that situation has changed. An explosion of recent research has illuminated the remarkable evolutionary success of lizards in New Zealand, and revealed a host of fascinating stories ... as well as grim tales of extinction, and uplifting narratives of bold and successful new approaches to conservation.

Two major groups—the geckos and the skinks—have evolved to exploit the opportunities available to a small scaly New Zealander. In the process, they have diversified into a stunning variety of animals, with an astonishing range of sizes, shapes, behaviours, and ecologies. Many skinks are sombre brown, but some are boldly patterned. The geckos take it further, with some species garishly adorned with vivid lime-green bodies, yellow eyes, and bright blue tongues. Some are heavyset, some are slender. Some are active by day, some by night. Some are forest dwellers, some live in the high cold grasslands, and some forage in the intertidal areas around seabird colonies. Most of them eat insects of one kind or another, but many have a fondness for nectar, and play an important ecological role in pollinating New Zealand's native plants.

The unique challenges of life in New Zealand have fashioned distinctive ecologies in lizards as well. In the cold climates that prevail, most lizards (geckos as well as skinks) reproduce by live-bearing rather than egg-laying; by keeping her babies within her body, a pregnant female can seek out the warmest places so her offspring develop more rapidly. But even so, pregnancy can be a drawn-out affair in the frigid high country of the South Island (sometimes lasting more than a year). Many New Zealand lizards live their lives at a slower pace than similar-looking species in other parts of the world. The giant Duvaucel's Gecko doesn't reach maturity until it is at least 6 years old and then produces a litter of two offspring every second year for the next 50 years or so. It's life in the slow lane. If you live in New Zealand, that small lizard you see in your garden may well be older than your children, and perhaps even older than you.

Taking things slowly and efficiently is a superb evolutionary strategy if you live on a cold island where sunlight and food are hard to find. In refuges where predators cannot threaten them, New Zealand lizards can attain remarkably high population densities. But that same slow-paced lifestyle is a catastrophe when humans arrive with their rats, cats, ferrets, stoats, and weasels. Slow reproductive rates mean that after it is hammered by exotic predators, a lizard population may never recover. And with no history of exposure to mammalian predators over evolutionary time, New Zealand's lizards have been sitting ducks for the ravenous newcomers. Fossil evidence, reviewed in this book, reveals that New Zealand has already lost some of its largest and most spectacular lizard species.

But there are good news stories also, amidst the doom and gloom. After decades of benign neglect, a virtual tsunami of taxonomic, ecological, and conservation-oriented research has swept over the New Zealand reptile fauna—led by the authors of the chapters in this book. Prompted by new technologies, new ideas, growing public interest, and a new generation of researchers, our knowledge of the New Zealand reptile fauna has increased dramatically. This book brings together that avalanche of information. It tells us what we know about New Zealand lizards, what we don't know, and how best we can go about understanding and conserving these remarkable animals.

The challenges are considerable. Small lizards still don't evoke the same thrill as a Kiwi or a Tuatara. Genetic research is telling us that many New Zealand lizards are restricted to very small areas, often on small islands where the twin threats of invasive predators and a changing climate may be catastrophic. But at the same time, we have learned an enormous amount about how best to study these animals and how to conserve them. New Zealanders have led the way in working out how to eradicate rats from offshore islands: a critically important conservation tool once regarded as impossible, but now used routinely around the world.

Most importantly, this authoritative volume brings together the experts on New Zealand lizards, to provide an exciting snapshot of a unique fauna. A fauna that was ignored for so long has now emerged from beneath the shadow of its renowned reptilian neighbour. And our new understanding of New Zealand lizards is not just relevant to local issues. In many ways, the New Zealand reptile fauna provides an ideal opportunity for research into broader issues of wildlife biology and faunal conservation and management. These are lizards with a distinctly iconoclastic New Zealand approach, breaking many of the rules by which the more orderly lizards of other continents live out their lives. The chapters in this book use New Zealand examples to challenge and extend modern ideas in fields as diverse as evolution, ecology, physiology, and adaptive management.

It's the book I wish I had all those years ago, when I encountered my first New Zealand lizard on Stephens Island.

School of Life and Environmental Sciences, Rick Shine
University of Sydney
Sydney, Australia
April 2016

Preface

I arrived in New Zealand in November 2004, fresh out of my PhD, to complete a postdoctoral fellowship at Victoria University of Wellington, in association with the Allan Wilson Centre for Molecular Ecology and Evolution. The aim of my postdoc was to investigate the phylogenetics, biogeography, and evolution of New Zealand skinks. Knowing virtually nothing about New Zealand lizards at this stage, I was stunned by both their ecological and species diversity, but conversely, by their lack of morphological diversity. Becoming familiar with the lizard fauna was a steep learning curve, hampered by the limited published information available on most New Zealand species and the relative inaccessibility of much of what was actually known. A substantial proportion of the knowledge of New Zealand lizards was contained within unpublished student theses, reports to the Department of Conservation, and other grey literature sources. This was in stark contrast to my native Australia, where there had been numerous authoritative field guides and other texts on its reptile fauna (e.g. the various editions of Harold Cogger's 'Reptiles and Amphibians of Australia'). Such summaries of the New Zealand lizard fauna were sadly lacking, apart from a few pocket guides (e.g. Gill and Whitaker's 'New Zealand Frogs and Reptiles').

I also became aware of the massive taxonomic impediment that was present in New Zealand. Forty-five lizard species were described at the time (28 skinks, 17 geckos), but a further 33 putative species were known, though not described. Thus, 43 % of the known lizard fauna was awaiting formal description. This not only masked the true diversity of the native lizard fauna, preventing broader global recognition of New Zealand as a lizard hotspot, but it failed to prompt the ecological, evolutionary, and physiological research that was required to enhance our knowledge of New Zealand lizard species. Hence, as I commenced my project on the origin and evolution of New Zealand skinks, I found myself, by necessity, drawn into taxonomic research. I rapidly developed a strong interest for the topic, and my taxonomic research continues through to today (see Chap. 4).

As I set about my background reading and literature searches for my postdoc project, I started taking notes on each scientific paper that I read. As the document quickly extended out to over 200 pages (and this was just for the skinks!!), I started to entertain thoughts about writing a book on New Zealand skinks. The initial idea was for something along the lines of the ornithological, Handbook of Australian, New Zealand and Antarctic Birds (HANZAB) series, which provides summary descriptions of all that was known about each species at the time of publication. But it quickly became clear that there were too many knowledge gaps for such an enterprise, and other research priorities (e.g. publishing papers, getting myself another postdoc/academic job) soon distracted my focus. Although I moved back to Australia in July 2007 to commence another postdoc, I continued to actively publish on New Zealand lizards over the next decade. But with the completion of Trent Bell's 'New Zealand Lizards Database' (http://nzlizards.landcareresearch.co.nz/Default.aspx), essentially an online HANZAB for all New Zealand lizard species, the idea slowly faded into the background.

That's how things remained until August 2014, when Springer contacted me about publishing a book on New Zealand reptiles. I had an academic job at Monash University (Melbourne, Australia), and as Alison Cree has recently published an amazingly comprehensive book on Tuatara (Cree 2014 Tuatara: biology and conservation of a venerable survivor. Canterbury University Press), it seemed like the timing was right for a similarly comprehensive book on the New Zealand lizards. Whilst the taxonomic impediment was still prevalent (57 described, and 47 undescribed, extant taxa), numerous molecular studies had provided strong support for the formal recognition of these putative taxa and clarified the phylogenetic relationships among species (see Chap. 4). But importantly, the book represented an opportunity to complete the first detailed synthesis of our knowledge of the New Zealand lizard fauna and make information from unpublished sources more widely available. I drew upon my network of friends and colleagues to write chapters on every aspect of the New Zealand lizard fauna, including the history of discovery, fossil record, taxonomy, biogeography, ecology, reproduction and life history, diseases, physiology, sampling methods, conservation, and invasive species. Each chapter, and indeed the overall book, aims to provide a synthesis of the current state of knowledge, identify key gaps, and stimulate and guide future research on New Zealand lizards.

Bringing the New Zealand lizard book to fruition involved the support, encouragement, and assistance of a plethora of people. Firstly, I'd like to thank Verena Penning and Dhayanidhi Karunanidhi from Springer for their invaluable help in putting the book together. Kelly Hare and Alison Cree provided advice during the initial planning stages of the book. I'll be forever indebted to Charlie Daugherty for providing me with the opportunity to work on New Zealand lizards and for taking a chance on me for my first postdoc. I've never had a research project more thoroughly supported, than during my time in New Zealand. I'm extremely appreciative of Peter Ritchie for his involvement in the skink research programme and for mentoring me on how to run a research programme and supervise graduate students. My skink research programme benefited from major contributions from Libby Liggins, Stephanie Chapple, Kelly Hare, Kim Miller, and Shay O'Neill. I thank the late Tony Whitaker for his amazing enthusiasm and for sharing his wealth of knowledge during my New Zealand lizard research. I also acknowledge my diverse array of collaborators, including Rod Hitchmough, Geoff Patterson, Dianne Gleeson, Dave Towns, Nicky Nelson, Trent Bell, Shawn Laffan, Giovanni Di Virgilio, and Reid Tingley. I thank Brian Gill, Raymond Coory, Benno Kappers, and Shai Meiri for their help and assistance during my New Zealand lizard research.

A special thank you to all of the contributors to the book and your efforts in summarising our currently knowledge of the New Zealand lizard fauna. This book was greatly improved through the input from a range of external reviewers for each chapter, including Kelly Hare, Rod Hitchmough, Marc Jones, Sue Jones, Nicky Nelson, Glenn Shea, Mike Thompson, Dave Towns, and Graham Wallis. I'm particularly indebted to Nicole Schumann for her assistance with copy-editing many chapters. Finally, this book would not have been possible without the endless love, encouragement, and support of my wife, Nicole, and daughter, Kira, as well as Daisy, Toby, and all of the other furred and feathered members of our family.

Clayton, VIC, Australia David G. Chapple

Contents

Chapter 1
Synthesising Our Current Knowledge of New Zealand Lizards

David G. Chapple

Abstract The New Zealand lizard fauna, comprising of skinks (Scincidae: Eugongylinae) and geckos (Diplodactylidae), is the most diverse squamate reptile assemblage of any cool temperate region on Earth. It is characterised by its ecological, evolutionary and physiological diversity, rather than its morphological diversity. New Zealand lizards have traditionally been underappreciated, and the recognised fauna (both described and undescribed) has almost trebled since the 1980s, from 38 to 104 taxa. A range of factors have delayed research and broader recognition of the New Zealand lizard fauna, particularly the fact that 45 % of recognised species remain undescribed. This book brings together the world's leading experts on this group of lizards to produce the first authoritative overview of the history, fossil record, taxonomy, biogeography, ecology, life history and reproduction, diseases, physiology, sampling methods and conservation of New Zealand lizards. In doing so, it highlights what is currently known, what is not and where future research efforts should be directed. It is hoped that by showcasing New Zealand lizards and the diverse array of ecological, evolutionary and physiological adaptations that the fauna possesses, the book will stimulate research on this group of lizards, particularly in the areas of greatest need or importance.

Keywords Biogeography • Conservation • Disease • Ecology • Fossil record • Gecko • Life history • Physiology • Reproduction • Sampling methods • Skink • Species discovery • Taxonomy

1.1 The New Zealand Lizard Fauna

Nestled in the south-west Pacific, New Zealand is a large archipelago that displays the faunal signatures of both its Gondwanan origins and more recent oceanic influences (Daugherty et al. 1993; Gibbs 2006). New Zealand was one of the last

---

D.G. Chapple (✉)
School of Biological Sciences, Monash University, 25 Rainforest Walk, Clayton, VIC 3800, Australia
e-mail: David.Chapple@monash.edu

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_1

countries on Earth to be discovered, and likewise, the full extent of the faunal diversity present within the archipelago is only just starting to be appreciated. This is no better exemplified than in lizards, with just 38 species (21 skinks, 17 geckos) recognised in the early 1980s (Newman 1982). This number has now increased to 104 extant species that are formally, or informally, recognised (61 skinks, 43 geckos; Hitchmough et al. 2016a, b). Whilst this ranks the native lizard fauna of New Zealand as one of the most diverse squamate reptile assemblages of any cool, temperate region on Earth, this diversity, along with the vast array of ecological, evolutionary and physiological adaptations exhibited by New Zealand lizards, has been largely underappreciated, both within the country and beyond its shores.

The presence of the tuatara (*Sphenodon punctatus*) in New Zealand, the sole survivor of a once diverse reptilian order (Cree 2014), may have diverted attention from the lizard fauna. After all, the New Zealand lizard fauna comprises skinks (Scincidae; Eugongylinae) and geckos (Diplodactylidae), which are common and widespread throughout the world, particularly in the Australasian and Pacific regions (Pianka and Vitt 2003; Wilson and Swan 2013; Cogger 2014). Our limited knowledge of New Zealand lizards might also be a matter of numbers; a relatively small human population (4.68 million as at April 2016; http://www.stats.govt.nz/tools_and_services/population_clock.aspx) means that there are comparatively few researchers to study such a diverse fauna. Indeed, there are only eight universities in New Zealand, though a substantial proportion of herpetological research has been conducted by government agencies (e.g. Department of Conservation, Landcare Research or the former Ecology Division, Department of Scientific and Industrial Research and Wildlife Service) and environmental consultants.

Whilst these factors have limited the volume of research that has been conducted on New Zealand lizards, much of what is known is also not freely available as it is contained within unpublished student theses, government reports, environmental consultant reports and other grey literature (Whitaker and Thomas 1989). Some information still remains in people's filling cabinets, on their computers or locked away in their minds. This book aims to collate all of this scattered knowledge into a single location and synthesise it into the first comprehensive summary of New Zealand's remarkable lizard fauna. It brings together the world's leading experts on the group to produce an authoritative overview of the history, fossil record, taxonomy, biogeography, ecology, life history and reproduction, diseases, physiology, sampling methods and conservation of New Zealand lizards. In doing so, it highlights what is known, what is not and where future research should be directed.

Unfortunately, no book on New Zealand lizards can escape the taxonomic impediment that currently exists. Museums, traditionally the drivers of taxonomic research throughout the world, have been strangely silent on New Zealand lizards. Aside from Charles McCann at the Dominion museum (Te Papa Tongarewa, Museum of New Zealand), who completed the only major taxonomic revision for the fauna (McCann 1955), taxonomic research has been left to university and government researchers, or unpaid enthusiasts (Shea 2016; Hitchmough et al. 2016b). Thus, just as it is problematic to study species that you are not aware exist, it is difficult to enhance your knowledge of a fauna if recognised species actually represent a complex of several species. Extreme examples of this are Hardy's (1977) *Leiolopisma nigriplantare maccanni* (McCann's *Leiolopisma zelandica*), which is now recognised as 19 distinct taxa, and McCann's (1955) *Hoplodactylus pacificus*, which has since been separated into 21 taxa (Table 1.1 lists the species recognised by McCann (1955) and Hardy (1977) and the taxa that are now recognised within each of these species; also see Chapple and Ritchie (2013)). This has made it difficult to link information between the composite taxa and currently recognised species. Such instances of uncertainty are highlighted throughout each chapter. Although there have been some disparate views on how to deal with the taxonomic impediment in New Zealand lizards (Jewell 2008; Chapple and Hitchmough 2009), all authors in this book follow the taxonomy outlined in the most recent Department of Conservation Threat List for reptiles (Hitchmough et al. 2016a). Since 45 % of the recognised, extant lizard fauna (104 species) remain to be described (Hitchmough et al. 2016b), this book follows the inherent practice in New Zealand of using tag names (e.g. *Dactylocnemis* 'Matapia Island', *Oligosoma* aff. *chloronoton* 'West Otago') when referring to these taxonomically indeterminate (unnamed or undescribed) taxa.

1.2 An Overview of *New Zealand Lizards*

The book comprises 12 contributed chapters covering every aspect of the biology of New Zealand lizards. In Chap. 2, Shea (2016) provides an authoritative overview of the history of discovery of New Zealand lizards, from first contact with Māori through to the present day. He discusses the distinct phases of species discovery and the factors that have influenced our understanding of lizard diversity in New Zealand. The chapter also provides an important historical context within which to consider the biology, ecology and conservation of the native lizard fauna. For instance, the first detailed study of a New Zealand lizard species was not conducted until the 1950s (Barwick 1955, 1959), illustrating just how much knowledge has been generated over the last six decades.

In Chap. 3, Worthy (2016) presents the first comprehensive review of the fossil material that exists for New Zealand lizards. Whilst the pre-Quaternary fossil record for lizards is limited, the Quaternary fossil record provides a vital indication of the prehuman diversity and distribution of New Zealand lizard species and a baseline with which to assess the impact of humans and introduced mammals on the native lizard fauna.

New Zealand lizards are characterised by their ecological and taxonomic, rather than morphological, diversity. Chapter 4 (Hitchmough et al. 2016b) provides an overview of the taxonomy of native skinks and geckos and the recent molecular work that has led to the almost trebling of the known lizard fauna over the last three decades. Chapter 5 (Chapple and Hitchmough 2016) demonstrates that geckos colonised New Zealand during the Eocene or Oligocene (40.2–24.4 mya), prior to

Table 1.1 A comparison of species recognised by McCann (1955) and Hardy (1977), the two major taxonomic reviews for New Zealand lizards and the species that are currently recognised (Hitchmough et al. 2016a, b)

Previous taxonomy	Current taxonomy
McCann (1955)	
Geckos	
Naultinus elegans **(4)**	*Naultinus elegans*
	Naultinus punctatus
	Naultinus grayii
	Naultinus 'North Cape'
Hoplodactylus duvaucelii	*Hoplodactylus duvaucelii*
Hoplodactylus pacificus **(21)**	*Dactylocnemis pacificus*
	Dactylocnemis 'Matapia Island'[a]
	Dactylocnemis 'Mokohinau'
	Dactylocnemis 'North Cape'
	Dactylocnemis 'Poor Knights'
	Dactylocnemis 'Three Kings'
	Toropuku stephensi
	Toropuku 'Coromandel'[a]
	Woodworthia chrysosiretica[a]
	Woodworthia maculata
	Woodworthia 'Central Otago'
	Woodworthia 'Cromwell'
	Woodworthia 'Kaikouras'
	Woodworthia 'Marlborough mini'
	Woodworthia 'Mount Arthur'
	Woodworthia 'Otago/Southland large'
	Woodworthia 'pygmy'[a]
	Woodworthia 'Southern Alps'
	Woodworthia 'southern mini'
	Woodworthia aff. *maculata* 'Muriwai'[a]
	Woodworthia cf. *brunnea*
Hoplodactylus granulatus **(8)**	*Mokopirirakau granulatus*
	Mokopirirakau 'Cascades'[a]
	Mokopirirakau 'Cupola'[a]
	Mokopirirakau 'Okarito'
	Mokopirirakau 'Open Bay Islands'[a]
	Mokopirirakau 'Roys Peak'[a]
	Mokopirirakau 'southern forest'
	Mokopirirakau 'southern North Island'
Heteropholis rudis	*Naultinus rudis*
Heteropholis tuberculatus	*Naultinus tuberculatus*
Heteropholis gemmeus	*Naultinus gemmeus*
Heteropholis stellatus	*Naultinus stellatus*
Heteropholis nebulosus	*Mokopirirakau nebulosus*

(continued)

Table 1.1 (continued)

Previous taxonomy	Current taxonomy
Heteropholis manukanus	*Naultinus manukanus*
Not discovered in 1955/recognised by McCann	*Tukutuku rakiurae*
	Mokopirirakau cryptozoicus
	Mokopirirakau kahutarae
	Hoplodactylus delcourti
Skinks	
Leiolopisma grande grande	*Oligosoma grande*
Leiolopisma grande otagense	*Oligosoma otagense*
Leiolopisma grande waimatense	*Oligosoma waimatense*
Leiolopisma fallai	*Oligosoma fallai*
Leiolopisma homalonotum	*Oligosoma homalonotum*
Leiolopisma suteri	*Oligosoma suteri*
Leiolopisma oliveri (**2**)	*Oligosoma oliveri*
	Oligosoma townsi
Leiolopisma smithi smithi (**2**)	*Oligosoma smithi*
	Oligosoma smithi 'Three Kings, Te Paki, Western Northland'
Leiolopisma smithi numerale	*Oligosoma smithi*
Leiolopisma festivum	*Oligosoma lineoocellatum*
Leiolopisma aeneum (**3**)	*Oligosoma aeneum*
	Oligosoma hardyi
	Oligosoma levidensum
Leiolopisma moco	*Oligosoma moco*
Leiolopisma zelandica (**19**)	*Oligosoma polychroma*
	Oligosoma aff. *polychroma* 'Clade 2'
	Oligosoma aff. *polychroma* 'Clade 3'
	Oligosoma aff. *polychroma* 'Clade 4'
	Oligosoma aff. *polychroma* 'Clade 5'
	Oligosoma inconspicuum
	Oligosoma aff. *inconspicuum* 'North Otago'[a]
	Oligosoma aff. *inconspicuum* 'Okuru'[a]
	Oligosoma burganae
	Oligosoma toka[a]
	Oligosoma repens[a]
	Oligosoma longipes[a]
	Oligosoma aff. *longipes* 'Southern'[a]
	Oligosoma aff. *longipes* 'Rangitata'[a]
	Oligosoma maccanni
	Oligosoma notosaurus
	Oligosoma stenotis
	Oligosoma tekakahu[a]
	Oligosoma microlepis[a]

(continued)

Table 1.1 (continued)

Previous taxonomy	Current taxonomy
Leiolopisma ornatum **(2)**	*Oligosoma ornatum*
	Oligosoma zelandicum
Leiolopisma dendyi	*Oligosoma nigriplantare*
Leiolopisma turbotti	*Oligosoma nigriplantare*
Leiolopisma lineoocellatum **(6)**	*Oligosoma lineoocellatum*
	Oligosoma aff. *lineoocellatum* 'South Marlborough'
	Oligosoma aff. *lineoocellatum* 'Mackenzie Basin'
	Oligosoma aff. *lineoocellatum* 'Central Canterbury'
	Oligosoma chloronoton
	Oligosoma aff. *chloronoton* 'West Otago'
Leiolopisma latilinearum	*Oligosoma striatum*
Leiolopisma infrapunctatum **(8)**	*Oligosoma infrapunctatum*
	Oligosoma aff. *infrapunctatum* 'Alborn'[a]
	Oligosoma aff. *infrapunctatum* 'Chesterfield'[a]
	Oligosoma aff. *infrapunctatum* 'cobble'[a]
	Oligosoma aff. *infrapunctatum* 'crenulate'
	Oligosoma aff. *infrapunctatum* 'Hokitika'
	Oligosoma aff. *infrapunctatum* 'Southern North Island'
	Oligosoma aff. *infrapunctatum* 'Westport'
Sphenomorphus pseudornatus **(3)**	*Oligosoma ornatum*
	Oligosoma roimata
	Oligosoma aeneum
Not discovered in 1955/recognised by McCann	*Oligosoma judgei*
	Oligosoma pikitanga
	Oligosoma taumakae
	Oligosoma 'Whirinaki'
	Oligosoma sp. 'Homer Tunnel'
	Oligosoma northlandi (extinct)
	Oligosoma acrinasum
	Oligosoma alani
	Oligosoma macgregori
	Oligosoma whitakeri
Hardy (1977)—skinks	
Cyclodina aenea **(3)**	*Oligosoma aeneum*
	Oligosoma hardyi
	Oligosoma levidensum
Cyclodina alani	*Oligosoma alani*
Cyclodina macgregori	*Oligosoma macgregori*
Cyclodina oliveri **(2)**	*Oligosoma oliveri*
	Oligosoma townsi
Cyclodina ornata **(2)**	*Oligosoma ornatum*

(continued)

Table 1.1 (continued)

Previous taxonomy	Current taxonomy
	Oligosoma roimata
Cyclodina whitakeri	*Oligosoma whitakeri*
Leiolopisma acrinasum	*Oligosoma acrinasum*
Leiolopisma chloronoton **(2)**	*Oligosoma chloronoton*
	Oligosoma aff. *chloronoton* 'West Otago'
Leiolopisma fallai	*Oligosoma fallai*
Leiolopisma grande	*Oligosoma grande*
Leiolopisma homalonotum	*Oligosoma homalonotum*
Leiolopisma gracilicorpus	*Oligosoma homalonotum*
Leiolopisma infrapunctatum **(8)**	*Oligosoma infrapunctatum*
	Oligosoma aff. *infrapunctatum* 'Alborn'[a]
	Oligosoma aff. *infrapunctatum* 'Chesterfield'[a]
	Oligosoma aff. *infrapunctatum* 'cobble'[a]
	Oligosoma aff. *infrapunctatum* 'crenulate'
	Oligosoma aff. *infrapunctatum* 'Hokitika'
	Oligosoma aff. *infrapunctatum* 'Southern North Island'
	Oligosoma aff. *infrapunctatum* 'Westport'
Leiolopisma lineoocellatum **(4)**	*Oligosoma lineoocellatum*
	Oligosoma aff. *lineoocellatum* 'South Marlborough'
	Oligosoma aff. *lineoocellatum* 'Mackenzie Basin'
	Oligosoma aff. *lineoocellatum* 'Central Canterbury'
Leiolopisma moco	*Oligosoma moco*
Leiolopisma nigriplantare nigriplantare	*Oligosoma nigriplantare*
Leiolopisma nigriplantare maccanni **(19)**	*Oligosoma polychroma*
	Oligosoma aff. *polychroma* 'Clade 2'
	Oligosoma aff. *polychroma* 'Clade 3'
	Oligosoma aff. *polychroma* 'Clade 4'
	Oligosoma aff. *polychroma* 'Clade 5'
	Oligosoma inconspicuum
	Oligosoma aff. *inconspicuum* 'North Otago'[a]
	Oligosoma aff. *inconspicuum* 'Okuru'[a]
	Oligosoma burganae
	Oligosoma toka[a]
	Oligosoma repens[a]
	Oligosoma longipes[a]
	Oligosoma aff. *longipes* 'Southern'[a]
	Oligosoma aff. *longipes* 'Rangitata'[a]
	Oligosoma maccanni
	Oligosoma notosaurus
	Oligosoma stenotis
	Oligosoma tekakahu[a]

(continued)

Table 1.1 (continued)

Previous taxonomy	Current taxonomy
	Oligosoma microlepis[a]
Leiolopisma otagense form otagense	*Oligosoma otagense*
Leiolopisma otagense form waimatense	*Oligosoma waimatense*
Leiolopisma smithi **(2)**	*Oligosoma smithi*
	Oligosoma smithi 'Three Kings, Te Paki, Western Northland'
Leiolopisma striatum	*Oligosoma striatum*
Leiolopisma suteri	*Oligosoma suteri*
Leiolopisma zelandicum	*Oligosoma zelandicum*
Not discovered in 1977/recognised by Hardy	*Oligosoma judgei*
	Oligosoma pikitanga
	Oligosoma taumakae
	Oligosoma 'Whirinaki'
	Oligosoma sp. 'Homer Tunnel'
	Oligosoma northlandi (extinct)

[a] A new discovery since 1955 or 1977, but has phylogenetic affinities with a taxon that was part of a composite species that was recognised in 1955 or 1977

Numbers in parentheses highlight the number of species now recognised that originally formed part of each composite taxon. Refer to Hitchmough et al. (2016b) for further details and explanation

the 'Oligocene drowning', whilst skinks reached New Zealand during the Miocene (~18.3 mya) via long-distance overwater dispersal from New Caledonia, along the Lord Howe Rise and Norfolk Ridge. Chapter 5 further outlines how biogeographic studies have long been hampered by two key factors: recent range contractions and local extinctions following the introduction of ~31 exotic mammalian species and a limited grasp on the true diversity and distribution of the endemic lizard fauna. It provides an updated perspective on the biogeography of the native lizard fauna, including revised biogeographic categories for each species.

New Zealand lizards occupy a broad range of habitats, from coastal beaches (0 m asl) to alpine scrub and scree (2200 m asl), as well as numerous offshore islands and rock stacks. However, Chap. 6 (Hare et al. 2016) illustrates that basic ecological information is still lacking for the majority of lizard species and that the ecological traits of many species are, by necessity, inferred from closely related, but better-studied, species. The chapter summarises our current knowledge on the diet, activity, behaviour and predators of New Zealand lizards, whilst highlighting a range of interesting ecological traits (e.g. seed dispersal and pollination, vocalisation). Chapter 7 (Cree and Hare 2016) outlines how New Zealand lizards live life in the slow lane (e.g. long-lived, late maturing, low reproductive output) and exhibit a high incidence of traits (e.g. viviparity, long gestations and prolonged pregnancies) that are relatively less common elsewhere in the world.

In Chap. 8, Gartrell (2016) provides the first detailed synthesis of the parasites and diseases of native and captive reptiles in New Zealand. This review provides important information, both for the health of wild populations and for captive populations that are part of conservation programmes. New Zealand possesses an incredibly diverse lizard fauna, particularly given its cool temperate climate. Chapter 9 (Hare and Cree 2016) examines the thermal and physiological adaptations that enable lizards to thrive in New Zealand. Physiology is vitally important for many aspects of conservation management and is likely to increase in importance in the context of current climate change.

New Zealand lizards are often cryptic and difficult to catch. Thus, New Zealand researchers have pioneered the development, or modification, of a wide range of approaches to catch and identify native lizard species. Chapter 10 (Lettink and Hare 2016) outlines the methods used to catch New Zealand lizards, including systematic searching, live trapping and artificial retreats.

Chapter 11 provides an overview of the conservation of New Zealand lizards (Towns et al. 2016). Lizards play a large role in the worldview of Māori, but were poorly appreciated by European settlers. In fact, New Zealand lizards remained without formal protection until the 1980s, an unfortunate delay as 83 % of the fauna is currently listed as threatened or at risk. The chapter summaries conservation efforts over the past three decades, providing case studies of the five skink species that have been continually managed since the 1980s. New Zealand is considered a world leader in species conservation, particularly due to its use of translocations and offshore island sanctuaries. Chapter 12 (Nelson et al. 2016) discusses the use of mainland sanctuaries for lizard conservation in New Zealand. The chapter focuses on two cases studies: one in a fenced sanctuary and the other in an unfenced sanctuary. The potential impacts of predatory mammals, birds and invertebrates are examined.

Despite the abundance of exotic lizards (99 species) intercepted entering New Zealand (Chapple et al. 2016a), only one, the plague skink (*Lampropholis delicata*), has successfully established and become invasive. Chapter 13 (Chapple et al. 2016b) outlines the Australian source region for the invasive New Zealand populations, its mechanism of spread across New Zealand, and the biology and ecology of the plague skink within the country. Biosecurity measures to prevent its spread to conservation-sensitive offshore islands are discussed.

In the final chapter (Chapple 2016), the current knowledge of the New Zealand lizard fauna is summarised. A critical assessment of New Zealand lizard research is provided, forming the basis for recommendations for the direction of future research.

References

Barwick RE (1955) Studies on the scincid lizard, *Leiolopisma zelandica* (Gray, 1843) with notes on *Leiolopisma aeneum* (Girard, 1857). Unpublished MSc thesis, Victoria University of Wellington, New Zealand

Barwick RE (1959) The life history of the common New Zealand skink *Leiolopisma zelandica* (Gray, 1843). Trans R Soc N Z 86:331–380

Chapple DG (2016) The future of New Zealand lizard research. Chap. 14. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Hitchmough RA (2009) Taxonomic instability of reptiles and frogs in New Zealand: information to aid the use of Jewell (2008) for species identification. N Z J Zool 36:59–71

Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Ritchie PA (2013) A retrospective approach to testing the DNA barcoding method. PLoS One 8:e77882. doi:10.1371/journal.pone.0077882

Chapple DG, Knegtmans J, Kikillus H, van Winkel D (2016a) Biosecurity of exotic reptiles and amphibians in New Zealand: building upon Tony Whitaker's legacy. J Roy Soc New Zeal 46:66–84

Chapple DG, Reardon JT, Peace JE (2016b) Origin, spread and biology of the invasive plague skink (*Lampropholis delicata*) in New Zealand. Chap. 13. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Cogger HG (2014) Reptiles and amphibians of Australia, 7th edn. CSIRO Publishing, Melbourne

Cree A (2014) Tuatara: biology and conservation of a venerable survivor. Canterbury University Press, Christchurch

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Daugherty CH, Gibbs GW, Hitchmough RA (1993) Mega-island or micro-continent? New Zealand and its fauna. Trends Ecol Evol 8:437–442

Gartrell B (2016) Diseases of New Zealand reptiles. Chap. 8. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Gibbs G (2006) Ghosts of Gondwana. The history of life in New Zealand. Craig Potton, Nelson

Hardy GS (1977) The New Zealand Scincidae (Reptilia: Lacertilia); a taxonomic and zoogeographic study. N Z J Zool 4:221–325

Hare KM, Cree A (2016) Thermal and metabolic physiology of New Zealand lizards. Chap. 9. In: Chapple DG (ed) New Zealand Lizards. Springer, Cham

Hare KM, Chapple DG, Towns DR, van Winkel D (2016) The ecology of New Zealand's lizards. Chap. 6. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hitchmough R, Barr B, Monks J, Lettink M, Reardon J, Tocher M, van Winkel D, Rolfe J (2016a) Conservation status of New Zealand reptiles, 2015. New Zealand threat classification series. Department of Conservation, Wellington

Hitchmough RA, Patterson GB, Chapple DG (2016b) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand Lizards. Springer, Cham

Jewell T (2008) A photographic guide to reptiles and amphibians of New Zealand. New Holland, Auckland

Lettink M, Hare KM (2016) Sampling techniques for New Zealand lizards. Chap. 10. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

McCann C (1955) The lizards of New Zealand. Gekkonidae and Scincidae. Dominion Mus Bull 17

Nelson NJ, Romijn RL, Dumont T, Reardon JT, Monks JM, Hitchmough RA, Empson R, Briskie JV (2016) Lizard conservation in mainland sanctuaries. Chap. 12. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Newman DG (1982) New Zealand herpetology. In: Proceedings of a symposium held at the Victoria University of Wellington, 29–31 Jan 1980. New Zealand Wildlife Service occasional publication No. 2, Wellington, 495p

Pianka ER, Vitt LJ (2003) Lizards: windows to the evolution of diversity. University of California Press, Berkeley, CA

Shea GM (2016) History of discovery of the New Zealand lizard fauna. Chap. 2. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Towns DR, Hitchmough RA, Perrott J (2016) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? Chap. 11. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Whitaker AH, Thomas BW (1989) New Zealand lizards: an annotated bibliography. Ecology Division, Department of Scientific and Industrial Research, Lower Hutt

Wilson S, Swan G (2013) A complete guide to reptiles of Australia, 4th edn. Reed New Holland, Sydney

Worthy TH (2016) A review of the fossil record of New Zealand lizards. Chap. 3. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapter 2
History of Discovery of the New Zealand Lizard Fauna

Glenn M. Shea

Abstract Knowledge of the New Zealand lizards began with the arrival of the Māori in the thirteenth century, who largely applied their ancestral Polynesian names and attitudes to lizards. These relied heavily on mythology and folklore. The first European discoverers in the eighteenth and early nineteenth centuries noted the presence of lizards without providing any further detail, and it was not until the 1820s that the first specimens were collected and the 1830s when these were formally named. The 1840s saw three scientific expeditions visiting the country: the French aboard the *Astrolabe* and *Zelée* (1840), the United States Exploring Expedition (1840) and the English Antarctic Expedition aboard the *Erebus* and *Terror* (1841). Together with the first major wave of settlement by the New Zealand Company, and by the French at Akaroa, significant herpetological collections began to arrive in museums in Europe and America, and many of the common New Zealand lizards were described, particularly by John Gray at the British Museum, Constant Duméril and Gabriel Bibron at the Museum national d'Histoire naturelle in Paris, and Charles Girard in Washington. This era ended in the 1860s with the Austrian *Novara* Expedition and a late flurry of descriptions by others. The formation of the New Zealand Institute in the late 1860s provided the opportunity for local naturalists to describe the fauna they collected, and Walter Buller, Frederick Hutton and William Colenso, in particular, began to describe new species. By the 1880s, when George Boulenger at the British Museum published his syntheses of the world's herpetofauna, a basic framework of local lizard diversity had emerged. After half a century during which little taxonomic work was done, a monograph of the local lizard fauna by Charles McCann provided the next platform for research and was followed by the burgeoning of field-based ecological studies. New revisions of the skink fauna began in the 1970s, with contributions by Joan Robb, Brian Gill, Graeme Hardy and Geoff Patterson, and emphasised the application of modern genetic techniques to field-based studies of different morphotypes, gradually refining previous concepts. Recent taxonomic study of the gecko fauna has progressed at a slower rate, with many species still to be formally described.

G.M. Shea (✉)
Faculty of Veterinary Science B01, University of Sydney, Sydney, NSW 2006, Australia
e-mail: glenn.shea@sydney.edu.au

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_2

Keywords Herpetological collections • Lizard • Naturalists • New Zealand • Scientific expedition • Species description • Taxonomy

2.1 Introduction

In presenting this history of discovery of the New Zealand lizard fauna, I have chosen to integrate both ends of the scientific process, covering the collection of the specimens (without which the species would not have been named), and the scientific process by which they were named and their evolutionary relationships explored. As with many landmasses relatively newly explored and settled, the early history, in particular, involved extensive interactions between collectors (visiting or resident) and scientists based in institutions in the Northern Hemisphere. It is important to track the movements of the early collectors, as their specimens were often recorded in Europe with only general details on collection localities (such as ‘New Zealand’ and ‘North Island’), at a time when the geography of New Zealand was little known outside of the country.

The history of discovery is a complex one, involving numerous changes in nomenclature over time (covered in more detail in Hitchmough et al. 2016). To simplify the story for the non-cognate reader at this point, it is important to keep in mind that all New Zealand skinks, no matter what genus they were originally described under, are currently considered to belong to the genus *Oligosoma* (Chapple et al. 2009). For many years, two distinct genera were recognised: one with a scaly lower eyelid (variously *Hinulia*, *Tiliqua*, *Lygosoma*, *Sphenomorphus* and *Cyclodina*) and one with a clear window in the lower eyelid (variously *Mocoa*, *Leiolopisma* and *Oligosoma*; Patterson and Daugherty 1995). For geckos, the situation is even more complex. While the green geckos have generally been placed in *Naultinus* (although South Island species were sometimes placed in a distinct genus *Heteropholis*), the brown geckos have been placed in a number of genera, firstly *Gehyra* and *Naultinus* and then for many years *Hoplodactylus*. Most recently, *Hoplodactylus* has been split into five different genera (Nielsen et al. 2011), with *Hoplodactylus* itself now restricted to just two species. For simplicity’s sake, my use of the vernacular term ‘brown geckos’ refers to the former wider sense of *Hoplodactylus*, while ‘green geckos’ applies to the modern sense of *Naultinus*. The various changes in generic nomenclature have also resulted in changes to the spelling of the species names over time, as species names based on adjectives have had to change gender to fit with the gender of the genus name with which they are combined.

2.2 Māori Knowledge of Lizards

Human knowledge of the New Zealand herpetofauna began from the first arrival of the Māori in the thirteenth century (see also Towns et al. 2016). They arrived with a familiarity with gekkotans and skinks from their Polynesian homelands and found in New Zealand the same two major lineages, to which they transferred some of the names they had previously used. In particular, 'moko' or 'mokomoko', a lizard, is derived from the 'moko' or 'mo'o' of many Polynesian dialects, a word that subsequently appeared in the scientific names of one of the New Zealand skinks (*Oligosoma moco*) and a Fijian skink (*Emoia mokosarinivekau*), as well as in the generic names *Mocoa* among skinks and *Mokopirirakau* among geckos. Within the broad category of moko, there were numerous entities represented by suffixes, many of them representing recognisable genera, or even species (Bauer and Russell 1987).

Other recognisable transfers of names are 'ngarara' and 'karara', a general name for any reptiles in Māori, equivalent to the Marquesan 'nganga' (a house lizard) and Tahitian 'arara' (a common lively lizard) (Taylor 1848; Tregear 1891; Best 1909; Beattie 1920; Hiroa 1949; Biggs 1981). More obscurely, 'kakariki', a term applied to the green geckos in Māori, may be equivalent to the Marquesan 'kakaa' (Tregear 1891).

The Māori invoked lizards in many of their myths and superstitions, again following closely from their Polynesian ancestors in many cases (D'Estrey 1892; Hamilton 1903). There was a particular fear of lizards, often especially linked to tree lizards such as geckos (particularly green geckos; Cooper 1851; McCann 1955). Again, this follows from a fear of lizards in Polynesia and eastern Melanesia (Lesson 1828; Gibbons and Clunie 1984). Possibly this was due to a perceived linkage with death, with beliefs that demons or 'atua' are manifested by the lizards and that these will enter the body of the afflicted person and devour their intestines (Yate 1835; Angas 1847; Colenso 1878). There may be an element of truth behind some of these beliefs, as outbreaks of salmonellosis have been linked to lizard vectors in New Zealand (de Hamel and McInnes 1971).

An alternative suggestion is that the fear of lizards derives from conflation of lizards with crocodiles and ancestral fear of such large reptiles in Southeast Asia and Melanesia (Best 1988; Skinner 1964; Downes 1937). Other Māori legends derive lizards from the god Punga, a descendent of Tangaroa, and the fear among the Māori instead being due to the ugly appearance of the lizards (Colenso 1878; Best 1909). Several other gods and demons were considered to be manifested in the form of various lizards (Tregear 1891; Best 1909; Hirao 1949).

There are also linkages in Māori folklore between geckos and birds. The green geckos were considered to have developed from the residual yolk in the hatched eggs of the green parakeet (also known as kakariki in Māori, possibly due to the bright green coloration it shares with the green geckos). Conversely, the migratory long-tailed cuckoo (*Eudynamys taitensis*), or koekoe, was thought to transform each year into a mottled brown lizard, which hibernated over winter before reforming into a bird (Tregear 1891; Fulton 1904; Best 1909).

The involvement of lizards in Māori mythology is manifested in Māori artwork, with lizard motifs being recorded as earthworks (Colenso 1878) and cave petroglyphs (Hamilton 1898; Skinner 1964; Fomison 2013), as well as on buildings (Best 1909; Skinner 1964; Barrow 1969; Lewis 1982), pendants (Hamilton 1903; Skinner 1964), canoes (Stutchbury 1996) and burial chests and coffins (Cheeseman 1907; Stutchbury 1996). The lizard is possibly also linked to the Māori facial tattoo, as both share the name ‘moko’ (Tregear 1891; Downes 1937).

Despite the fear of some lizards, there is evidence that some Māori were willing to eat lizards, particularly the larger species (Shortland 1856; Crawford 1880; Hector and Tregear 1899; Tregear 1904; Beattie 1920). Together with land clearing, and predation by cats, introduced with European settlement (Taylor 1848, 1870; Stack 1874; Kirk 1896; Bathgate 1922), and the Polynesian rat (the kiore, *Rattus exulans*) (Whitaker 1973; McCallum 1986), brought with the Māori, this may have resulted in relatively recent local or complete extinction of some of the larger lizards that are now only known from very early historical specimens (Bauer and Russell 1986) or subfossil remains (Gill, 1985; Worthy 1987, 1991; Bauer and Russell 1988, 1990; see also Worthy 2016). Although some of the Māori reports of large lizards not now present in the fauna may reflect recently extinct taxa (Bauer and Russell 1987), or confusion between lizards and the larger tuatara by reporters of Māori mythology (Andrews 1986; Bauer and Russell 1988), some of the legends involving interactions between large lizards and Māori (particularly the taniwha and kumi) are clearly not based on reality due to the huge size of the reported animals (e.g. Colenso 1878; Downes 1937).

2.3 First European Exposure to New Zealand Lizards (1770–1827)

Some of the very earliest European voyages that reached New Zealand reported lizards, but without many details. Although James Cook did not mention lizards on his first voyage, when the *Endeavour* visited New Zealand between October 1769 and March 1770, the next few voyages reaching New Zealand did note them.

The French vessel *St Jean Baptiste*, with Jean-Francois-Marie de Surville (18.i.1717–1770.iv.7; Dunmore 1990) as captain, Guillaume Labé as First Lieutenant and Jean Pottier de l’Horme (8.vii.1738–?) as Second Lieutenant, arrived in New Zealand at Lauriston Bay (Cook’s Doubtless Bay) on 17 December 1769 (just a few days after Cook) and remained there for two weeks. Pottier de l’Horme reported ‘un petit lézard noir qui pouvait avoir 4 pouces de long’ (a little black lizard about four inches long) and de Surville’s log recorded a ‘few lizards’ (Dunmore 1981; Pottier de l’Horme 1914). De Surville died before the ship returned to France, drowning in heavy seas off Peru in April 1770. The vessel was then impounded for three years by the Spanish at Callao before Labé took the remaining members of the expedition home, arriving at Lorient in France on 23 August 1773 (Dunmore 1981).

Cook's scientists took slightly more notice of the herpetofauna on his later voyages. During the second voyage, in the *Resolution* and *Adventure*, which explored Antarctica and the Southern Pacific, the expedition visited New Zealand on three occasions in 1773–1774. Johann Reinhold Forster and his son Georg were the official naturalists, but the only mention of lizards came from the astronomer William Bayly (1738–1810.xii.21; Howse 2004) aboard the *Adventure*, who noted 'a few small harmless lizards' in the woodlands around Queen Charlotte Sound (Bayly 1914). The *Adventure* was at Queen Charlotte Sound from 7 April to 7 June 1773 and the *Resolution* from 18 May. Both ships spent most of their time in Ship Cove.

During his third voyage (in the *Resolution* and *Discovery*), Cook visited New Zealand en route to the North Pacific between 12 and 25 February 1777 and noted 'two or three sorts of small harmless lizards' (Cook 1784). This observation probably originates with the naturalist of the expedition, William Anderson (28.xii.1750–1777.viii.3; Keevil 1933), who made the same statement in describing the fauna in Queen Charlotte Sound (Anderson 1967). Both Anderson and Cook died during the expedition, Anderson dying of tuberculosis in the Bering Sea and Cook killed in Hawaii, and any specimens that might have been collected are now unidentifiable. Anderson's manuscript zoological notes do not contain any formal description of lizards of New Zealand origins (although Shea (2000) was unable to identify Otakoo, an island from which Anderson described *Lacerta affinis Gecko*, and suggested it may have been one of the New Zealand islands, Anderson's Otakoo is Takutea in the Cook Islands; Kloosterman 1976).

The next Europeans to observe New Zealand lizards were part of the French expedition commanded by Louis Isidore Duperrey aboard *La Coquille*, with naturalists René-Primevère Lesson (20.iii.1794–1849.iv.28) and Prosper Garnot (1794–1849) (Andrews 1986, 1993; Lescure 2015) on board. Garnot (weakened by dysentery in South America earlier in the expedition) remained in Sydney (Lescure 2015), leaving Lesson as the sole naturalist for New Zealand. The expedition stayed at the Bay of Islands from 3 to 17 April 1824. Sadly, Lesson made no comment on the lizards observed there when describing the herpetological discoveries of the voyage other than to note 'une seul espèce de Scinque que les naturels nomment Ngarara' (a sole species of skink which the natives name Ngarara; Lesson 1828, 1830). Later (Lesson 1839), he expanded this to 'quelques petites espèces de lézards' (several small species of lizards). However, he appears not to have collected any, as there are no New Zealand lizard specimens obtained by the expedition in the Museum National d'Histoire Naturelle in Paris (Duméril and Bibron 1836, 1839). Andrews (1986) stated that Lesson reported a blue-tailed striped skink (by implication from New Zealand), but this reference is to *Emoia cyanura*, described from specimens collected by the expedition in Tahiti.

In 1827, the *Astrolabe* (renamed from *La Coquille*) revisited New Zealand under the command of Jules Sébastien César Dumont D'Urville (23.v.1790–1842.v.8), with Pierre-Adolphe Lesson (1805–1888, Rene's brother), Jean-René Constant Quoy (10.xi.1790–1869.vii.4) and Paul Gaimard (31.i.1793–1858.xii.10) as naturalists. As well as being captain, D'Urville was a skilled botanist and had been second in command on the *La Coquille* expedition. New Zealand landfall was reached on 15 January 1827 in Tasman Bay. The east coast of the North Island, including Tolaga Bay (Baie Houa-Houa), Hauraki Gulf (Baie Shouraki) and the Bay of Islands, was visited before the expedition departed on 19 March. Despite this extensive period in the region, there is no mention of any reptiles having been collected other than two somewhat contradictory statements (while at the Bay of Islands): firstly, in D'Urville's narrative, that the islands have 'seulement quelques lézard assez gros' (only some rather large lizards) and secondly a comment in the same volume provided by Quoy, reporting general impressions of the natural history of New Zealand, that 'sauf quelques petites espéces de lézards, nous ne connaissons point d'autres reptiles' (except for some little species of lizards, we do not know of other reptiles) (Dumont d'Urville 1830). Indeed, although the separate four volume zoological account of the voyage includes chapters on mammals, birds, fish, molluscs and zoophytes, there is no section covering reptiles, and the general account of the zoology of the voyage (Volume 4 of the Zoologie) does not mention reptiles at all, suggesting a lack of interest in collecting this group of organisms.

2.4 First Specimens (1826–1843)

In Paris, André Marie Constant Duméril (1.i.1774–1860.viii.14), professor of ichthyology and herpetology at the Muséum national d'Histoire naturelle, had recently acquired a brilliant assistant, Marie Gabriel Bibron (20.x.1805–1848.iii.27) (Fig. 2.1). Together, they began producing in 1834 their masterwork, the nine-volume *Erpétologie Générale*, *ou Histoire Complète des Reptiles*, a monograph of the world's known reptile and amphibian fauna (Bour 2012). Volume 3, which included geckos, appeared in 1836 and contained a description of '*Platydactyle*' [*Platydactylus*] *Duvaucelii* (now *Hoplodactylus duvaucelii*), the largest extant New Zealand gecko. The species was described from many ('plusiers') specimens sent from Bengal to the Paris Museum by the naturalist Alfred Duvaucel (Duméril and Bibron 1836; Guibé 1954). It was only recognised 97 years later that the species was not Indian, but from New Zealand (Smith 1933a, b; Stephenson 1948), making the source of Duvaucel's specimens a mystery.

Alfred Duvaucel was born in 1793 in Évreux, France, and travelled to India to collect natural history specimens, arriving in Calcutta in May 1818. Together with Pierre-Médard Diard, he collected specimens around the Chandernagore region in Bengal, a post of the French East India Company. By the end of that year, they were accompanying Stamford Raffles on his expeditions and visited Penang, Singapore and Sumatra (G Cuvier 1821). Duvaucel then returned to Bengal and Benares (F Cuvier 1824), dying in Madras in August 1824 (Anonymous 1825), possibly

Fig. 2.1 Early authors of New Zealand lizard descriptions. (**a**) André Marie Constant Duméril (Image: Wikimedia Commons); (**b**) Gabriel Bibron (Image from Duméril et al. 1854); (**c**) Thomas Bell (Image: Natural History Museum, London, 051945); (**d**) John Edward Gray (Image: Natural History Museum, London, 001304)

due to mauling by a tiger (Anonymous 1835). He never visited New Zealand, and it is not known how specimens of *Hoplodactylus duvaucelii* reached India for Duvaucel to send them to Paris prior to his death. The description of the species by Duméril and Bibron in 1836 notes that the specimens even then were faded from long exposure to alcohol ('Nos individus paraissent avoir perdu leur couleur par l'effet de l'alcool'), suggesting they were not recently received at that time. None of the early French expeditions of discovery travelled from New Zealand to India, and hence the Bengal source presumably reflects either a contemporary error in recording of the source or an unknown trading link of natural history specimens with India in the earliest days of European settlement in New Zealand.

Shortly after Duvaucel's specimens reached Paris, the first specimen destined for a British collection was collected. Samuel Stutchbury (15.i.1798–1859.ii.12) (Fig. 2.2) was born in London and trained in medicine. After a few years working for William Clift at the Museum of the Royal College of Surgeons (where Richard Owen would later become curator), Stutchbury was employed by the Pacific Pearl Fishing Company as naturalist on their expedition to the South Pacific. He travelled to Sydney aboard the *Sir George Osborne* and transferred to the second ship, the *Rolla*, for departure from Sydney on 8 March 1826. Travelling via the Bay of Islands in New Zealand to Polynesia, he rejoined the *Sir George Osborne* in Tahiti for return to England. The expedition was in the Bay of Islands from 23 March to 4 April, and Stutchbury's journal (Stutchbury 1996) reports him spending much time ashore collecting during this period. On return to London, Stutchbury was appointed curator of the museum of the Bristol Institute. In 1850, he was appointed as a geological surveyor to the New South Wales Government. His health suffered during the long expeditions he made within Australia and from the criticism of his work by other local geologists. A broken man, he returned to Bristol in 1855 and died there a few years later (Branagan and Vallance 1976; Branagan 1983, 1993; Crane 1983).

The collections made by Stutchbury in the South Pacific were mostly marine (shells and corals) or ethnological in nature (Stutchbury 1996; Crane 1983). However, they did include one gecko specimen, which was received by the British Museum in 1830 (Gray 1843), where it was recorded with the locality 'Islands of the Pacific Ocean'. John Edward Gray (12.ii.1800–1875.iii.7) (Fig. 2.1), at the time a temporary assistant at the British Museum (he had been since 1824; Gunther, 1975), described this gecko as *Gehyra pacifica* in a short paper in the *Annals and Magazine of Natural History* (Gray 1834). Later (Gray 1842a), he transferred it to *Naultinus*, a genus which he more formally erected in a subsequent paper (Gray 1842b) in the same issue of his privately published journal, the *Zoological Miscellany*. It was not until the receipt of subsequent specimens from New Zealand (Gray 1843) that the distribution was able to be corrected and the species recognised as being from New Zealand.

Charles Darwin (12.ii.1809–1882.iv.19), aboard the *Beagle*, also visited the Bay of Islands for a very short stay between 21 and 30 December 1835. His herpetological collections were described in the expedition report by Thomas Bell (11.x.1792–1880.iii.13) (Fig. 2.1). Bell was a London dental surgeon and professor of zoology at King's College (Adler 1989) and had a particular interest in tortoises. He may have been invited to work on the reptiles because of the Galapagos tortoises Darwin had collected. Bell's (1843) description of the green gecko *Naultinus grayii* from Darwin's collection was accompanied by an illustration drawn by Benjamin Waterhouse Hawkins (1807–1894; Adler 2014), the first published illustration of a New Zealand lizard.

Fig. 2.2 Early collectors of New Zealand lizards. (**a**) Samuel Stutchbury (Image: State Library of New South Wales, P2/Stutchbury, Samuel); (**b**) Charles Pickering (Image: Wikimedia Commons); (**c**) Alexander John Smith (Image: Victorian Parliamentary Library); (**d**) Henry Edwards (Image: Wikimedia Commons)

2.5 The Age of Expeditions (1838–1858)

Shortly afterwards, Duméril and Bibron (1839) were penning the fifth volume of their *Erpétologie Générale*, which covered skinks. They described, in addition to the skinks in their own collection, the new species *Lygosoma moco* based on 'numerous specimens' from New Zealand in the collection of the Zoological Society of London. Duméril and Bibron had found the unpublished species name *moco*, created by Gray, associated with the specimens there (see also Gray (1845b), where it is listed as his manuscript name *Tiliqua moko* in the synonymy of his species *zelandica*). Gray, still wishing to integrate the word moco in one of his names, instead formed a new genus *Mocoa*. While the French naturalists and Gray worked largely independently in their home institutions, they visited collections in the other countries on several occasions. Gray visited the Paris Museum at least in 1826, 1832 and 1834 (Gunther 1975), while Bibron had visited London in 1838 and in several other years (Wheeler 1997; Bour 2012), and each had seen specimens labelled by the other. A handwritten catalogue of the Zoological Society's herpetological collections, dating from 1838 (Wheeler 1997), gives only one source of reptile specimens from New Zealand: a collection presented by the New Zealand Association (the predecessor to Wakefield's New Zealand Company), which operated between May 1837 and July 1838 (McLintock 1966; Burns 1989). Any lizards collected within this time period were likely to be from North Island, where the only long-term settlers were located.

Gray, newly promoted to keeper of the zoology department in the British Museum in 1840 (Gunther 1975), next received material collected by Johann Karl Ernst Dieffenbach (27.i.1811–1855.x.i). Ernst Dieffenbach was a political refugee from Germany who arrived in England in 1837 after completing his medical studies in Zurich and who rapidly came to the attention of scientific circles there, meeting Darwin and Richard Owen among others (Bell 1976; McLean 1990). Owen had just recognised the existence of moas (from fragmentary remains) and was keen to obtain more material, and Dieffenbach, possibly encouraged by Owen and Darwin, accepted a position as naturalist with the fledgling New Zealand Company. He arrived in New Zealand aboard the *Tory* on 17 August 1839 (landing at Ship Cove in Queen Charlotte Sound, where Cook had previously anchored) and successively explored around the Marlborough Sounds, Port Nicholson, Cook Strait, Taranaki (climbing Mt Egmont), the Chatham Islands and the Hutt Valley, before visiting New South Wales between September and October 1840. On his return to New Zealand, he initially explored the area around Auckland, before travelling down the coast to Tongariro and returning to Auckland via Thames (Dieffenbach 1843; Godley 2004). He returned to England in October 1841, where he wrote his two-volume book, *Travels in New Zealand*, published in 1843 (McLean 1990). Dieffenbach lived a precarious existence in England for the next several years before returning to Germany in 1848, his political activities forgiven. He died of typhus just seven years later.

Dieffenbach's natural history interests were primarily in birds and flora, although he did collect some lizards, which he sent to Richard Owen (20.vii.1804–1892.xii.18) at the Royal College of Surgeons. Owen, in turn, passed them on to Gray at the British Museum. From this material, Gray (1842b) described *Naultinus elegans* based on a specimen from Auckland (although he also mentioned unspecified material in the collection of the Zoological Society of London—presumably, like the types of *Lygosoma moco*, also from the New Zealand Association's collections). Gray (1843), in an appendix to Dieffenbach's *Travels*, described the skinks *Tiliqua zelandica* and *Tiliqua ornata*, both from Cook's Strait, and Gray (1845b) later added *Naultinus granulatus*, from an unspecified locality (based in part on a specimen that he had believed to be a distinct variety of *N. pacificus* in 1843). Gray (1843) also described *Naultinus punctatus* from a specimen donated by Surgeon H. Kelsall of the Royal Navy. The specimen was held in the collection of the Museum of Haslar Hospital (the museum of the Navy Medical Service), but was later donated to the British Museum by Sir John Richardson, curator of the Haslar collection (Gray 1845b).

Kelsall was presumably Henry Kelsall (1802–1874.xii.3) of the Royal Navy, the surgeon supervising immigrants and convicts aboard four ships between 1834 and 1842: the *Andromeda* (arriving in Sydney, 17 September 1834), the *Margaret* (arriving in Sydney, 30 May 1837), the *Juliana* (wrecked at the Cape of Good Hope with Kelsall and the immigrants reaching Sydney aboard the *Mary Hay* on 19 May 1839) and the *Waterloo* (again wrecked at the Cape of Good Hope, with Kelsall and the convicts arriving in Hobart aboard the *Cape Packet* on 23 November 1842, before Kelsall, travelling alone, reached Sydney aboard the *Moffatt* on 24 December 1842). There is no record that Kelsall ever visited New Zealand, but he may have acquired the specimen from traders while in Sydney.

The next, and largest, collections of New Zealand lizards to reach Gray came from the Antarctic Expedition of 1839–1843. Conducted in the ships *Erebus* and *Terror*, under the command of Sir James Clark Ross, the main aims were to map magnetic fields and explore the Southern Ocean and Antarctic. Between its two long explorations of Antarctic waters, the expedition visited the Bay of Islands, near Paihia, from 17 August to 23 November 1841 (Shea 1995).

The official naturalist aboard the expedition was Robert McCormick (who had earlier been naturalist on the first leg of the *Beagle* expedition), and the botanist was Joseph Dalton Hooker. Gray also had an unofficial source of specimens: his nephew, Lieutenant Alexander John Smith (21.xii.1812–1872.ix.7), aboard the *Erebus* (Gray 1845a; Boumphrey 1964). Smith (Fig. 2.2) was the second son of Gray's brother-in-law, Lord Henry Smith (the first name was not a title!), and had previously sailed on three ships of the Royal Navy. Following the expedition, Alexander Smith returned to Australia as officer in charge of the observatory at Hobart. Later, he went to the Victorian goldfields, becoming Gold Commissioner in 1853. In 1861, he was elected to the Victorian Legislative Assembly, before retiring to his property, Langley, in 1864 (Boumphrey 1964).

On the return of the expedition to England in September 1843, Gray compiled two major works: a report on the herpetological results of the Antarctic Expedition, which he intended to become a broader monograph on the reptiles of Australia and New Zealand, and concurrently, his *Catalogue of the Lizards in the Collection of the British Museum*. Unfortunately, funding ran out for the expedition report, and only the first part appeared (in 1845, in the same year as Gray's lizard catalogue). The plates relating to the New Zealand lizards (drawn by the brilliant artist George Henry Ford, 1809–1876; Adler 2014) did not appear in this part and were not published until 1867, when Gray produced a new treatment of the Australian and New Zealand lizards (Gray 1867). The final part of the herpetology of the Antarctic Expedition report did not appear until 1875, after Gray's death, when the remaining plates were accompanied by a new text, written by Gray's successor, Albert Günther (Shea 1995). Because of these delays in publishing most of the expedition report, the brief descriptions in Gray's (1845b) *Catalogue* represent the original descriptions of most of the species collected by the Antarctic Expedition, even though Gray's *Catalogue* cites the descriptions as having been published in the *Zoology of the Erebus and Terror*.

Based on the Antarctic Expedition material, Gray (1845b) described the skink *Mocoa smithii* (named for his nephew and the species best represented in the collections), but also found among the expedition's collections additional specimens of the skink *Mocoa zelandica* and the geckos *Naultinus pacificus*, *Naultinus elegans* and *Naultinus grayii*, allowing him to redescribe these species in the same monograph.

In an appendix to his *Catalogue*, Gray reported on some additional New Zealand lizards, received from a Mr Earl, and from these described the skink *Mocoa grandis*. Earl's collection, received after Gray had written the manuscript for the main body of his *Catalogue*, also contained six gecko specimens. One of these contributed a second specimen to the description of the brown gecko *Naultinus granulatus*, and the other five were used to define two more gecko taxa, tentatively ascribed the manuscript names *brevidactylus* and *maculatus* in the appendix, although Gray at the time considered both to be varieties of *N. pacificus* (*maculatus* would eventually become recognised as a valid species, while the identity of *brevidactylus* remains unresolved).

Percy William Earl (13.vii.1811–1846.iv.24) was born in London, the son of a ship's captain, and was sent to sea early to learn his father's trade (Scofield et al. 2012). He came to New Zealand in 1842 (after previous voyages to Australia and America) with the intention of making a living as a natural history collector, arriving at Port Nicholson on 24 September aboard the *Nelson*. He initially collected around Wellington, but after a visit to Akaroa in March 1843, spent about 15 months in Otago. He returned to Wellington about August 1844 and departed for England shortly thereafter, leaving New Zealand on 15 October aboard the *Bella Marina*. He took with him six cases of natural history specimens (many of them likely filled with moa bones) and sold his specimens to the British Museum in early January 1845, just in time for late inclusion in Gray's Catalogue. Sadly, Earl died the following year after another brief trip to Australia, drowning in a shipwreck in Torres Strait.

The final new species contributed by Gray in his *Catalogue* was also listed in the appendix: the skink *Mocoa owenii*, described from a single specimen from the Royal College of Surgeons and, hence, presumably from Owen. This may have been the residue of Dieffenbach's material. This species has subsequently been considered synonymous with *Oligosoma moco*.

In addition to these new species, Gray had access to a few other green gecko specimens at the Museum, which he listed in his *Catalogue* (Gray 1845b): three individuals of *Naultinus grayii* from 'Mr Egerley's collection' and one *Naultinus elegans* from 'W.E. Cormack'. John Egerley (1814–1849.vi.9), more usually spelt Edgerley, arrived in New Zealand in 1835 as gardener and botanist to the new British Resident, Lieutenant Thomas McDonnell. Settling at Horeke, McDonnell and Edgerley explored Kaipara Harbour (first visiting the Bay of Islands to obtain permission from the Māori chiefs for their expedition) and, later, other parts of

North Island. Edgerley visited England in 1842, bringing with him plants for Hooker at Kew (and presumably the lizards for the British Museum). He returned to New Zealand the following year, settling at Newmarket and developing a nursery, before dying at the young age of 35 (Cooper 1970).

William Eppes Cormack (5.v.1796–1868.iv.30) is better known for his explorations and natural history collections from Newfoundland, Canada (Story 1976). He later settled in New Zealand, arriving in 1839 and buying land in the Waikato and Waipo River valleys in competition with the New Zealand Company. After a short period in England in 1843 to discuss with his backers his difficulties with the land titles he had bought, he settled in Auckland, where he ran a watchmaking business. He left New Zealand for England in 1849 aboard the *Dorset*, after which he visited California before settling in Canada again (Fardy 1985).

At about the same time as the Antarctic Expedition was exploring the Southern Ocean, the United States Exploring Expedition of 1838–1842 was exploring the Pacific (Stanton 1975). Under the command of Captain Charles Wilkes, this expedition visited the Bay of Islands in 1840 (18 months before the Antarctic Expedition) and collected several lizard specimens. While the ships of the expedition did not arrive in New Zealand until 30 February (on return from their exploration of the Southern Ocean and the Auckland Islands), the expedition scientists had travelled independently from Sydney and had been at the Bay of Islands since 24 February (Wilkes 1845). Together again, the expedition departed New Zealand on 6 April.

The herpetological results of the US Exploring Expedition were compiled by Charles Girard (9.iii.1822–1895.i.29) (Fig. 2.3), a Swiss-born zoologist who had followed his mentor, Louis Agassiz, to the USA and had been employed as an assistant at the recently established Smithsonian Institution (Adler 1989). Girard described the skink species *Cyclodina aenea*, *Hombronia undosa*, *Hombronia fasciolaris* and *Lygosomella aestuosa*, and the gecko *Hoplodactylus pomarii*. He also redescribed Gray's *Tiliqua zelandica* (under the name *Oligosoma zelandicum*), as well as *Naultinus punctatus* (Girard 1857, 1858), all based on material collected during the expedition. While all of these are reported as being from the Bay of Islands, some mislabelling of the collection seems to have taken place, with some specimens missing and others seemingly not representing the species described (Zug 1985).

Girard's taxonomic conclusions were largely rejected by later workers, with only *Cyclodina aenea* still recognised as a distinct species today. His generic conclusions were even more problematic, with *Cyclodina aenea* and *Hombronia undosa* (considered to represent two different genera by Girard) subsequently recognised as the same species (Hardy 1977). However, by naming multiple genera among the New Zealand skinks at such an early time, Girard did have a lasting impact. His generic names *Oligosoma* and *Cyclodina* were used for many years, and with recent revisionary work, *Oligosoma* has become the generic name for the entire New Zealand skink lineage (Chapple et al. 2009).

Girard (1858) recorded Charles Pickering (the zoologist aboard the *Vincennes*, the expedition's flagship) as the collector of most of the New Zealand lizards,

Fig. 2.3 American and European authors of New Zealand lizard descriptions, 1857–1906: (**a**) Charles Girard (Image: from Goode 1891); (**b**) Edward Drinker Cope (Image: Wikimedia Commons); (**c**) George Albert Boulenger (Image: Natural History Museum, London, 051989); (**d**) Samuel Garman (Image: Ernst Mayr Library, Museum of Comparative Zoology, Harvard University)

although the type specimen of *Hoplodactylus pomarii* was specifically noted as having been donated by King Pomare, leader of the Ngapuhi at Otuihu— one of the few documented contributions by the Māori to early herpetological collections. Pickering (10.xi.1805–1878.iii.17) (Fig. 2.2) was a medical practitioner trained at Harvard and librarian and curator at the Academy of Natural Sciences in Philadelphia prior to the expedition. Afterwards, he travelled in Africa and the Middle East, before returning to medical practice in Boston (Staphleu and Cowan 1983). He is better known for his polygenist views, as espoused in his anthropological report for the expedition (Pickering 1848). The lizards were drawn at the time of collection by the expedition's artist Joseph Drayton (1795–1856; Adler 2014).

2.6 A Swansong from the French (1851–1868)

The early 1840s saw an attempt by the French to set up a settlement on the South Island, partly to support the French whaling industry in the surrounding seas. The Nanto-Bordelaise Compagnie (company) was created to bring in French settlers, who arrived in New Zealand on 9 July 1840 aboard the *Comte de Paris*, preceded by its consort, the French naval vessel *L'Aube* (Buick 1928). Eventually settling at Akaroa on the Banks Peninsula, the French immigrants were accompanied by the experienced naturalist Pierre Joseph Sainte Croix Croquet de Belligny (26. iii.1810–1877). Born in Guadeloupe, de Belligny was initially appointed by the Jardin des Plantes in Paris as the Garden's Travelling Correspondent for the colony (Simpson 1983), but soon after arrival, he became the local agent for the Nanto-Bordelaise Compagnie, which limited his time for natural history collecting.

L'Aube departed Akaroa in January 1843, taking with it seven cases of natural history specimens collected by de Belligny (Proust de la Gironière 2002). Its replacement, *Le Rhin*, arrived on 11 January 1843, with Louis Arnoux (15. iv.1814–1867.ii.3) on board as chief surgeon. He would also collect natural history specimens.

De Belligny departed from Akaroa on 19 April 1845 aboard the whaler *Pallas* for France; *Le Rhin* departed, with Arnoux, on 16 April 1846. Following his return to France, de Belligny was posted to diplomatic positions in Zanzibar, Manila and the USA, before dying in Lausanne in 1877 (Proust de la Gironière 2002).

Between them, de Belligny and Arnoux donated several lizards from New Zealand to the collection of the Muséum National d'Histoire Naturelle in Paris. Four of these were described by Constant Duméril and his son Auguste (Duméril and Duméril 1851) (Constant's son had been co-opted following Bibron's early death from tuberculosis) as a new species of skink, *Lygosoma lineoocellatum*. Although recorded as originating from Tasmania, as several other specimens provided by de Bellingy and Arnoux, the species is from New Zealand, and there is no evidence that either collector ever travelled to Tasmania. The confusion over the locality may be due to a rarity of direct transport from Akaroa to France, with transport from Akaroa to nearer ports like Hobart more common, and the specimens having to be trans-shipped for the longer voyage to Europe. A similar issue with mislabelling occurred with another Arnoux specimen; Duméril and Duméril (1851) described a gecko, *Gymnodactylus arnouxii*, purportedly from New Zealand, although the species is from the South Pacific. This likely reflects the visit of *Le Rhin* to French missions in Tonga, Wallis and Futuna, and New Caledonia between May 1844 and January 1845.

An Arnoux or de Belligny specimen from Akaroa is likely to be the basis for another New Zealand species. This time, the describer was an American, the famous zoologist and palaeontologist Edward Drinker Cope (28.vii.1840–1897.iv.12). Cope (Fig. 2.3) had recently returned in 1864, aged just 24, from a tour of European museums that had opened his eyes to the diversity and systematics of modern reptiles, meeting most of the major figures in herpetology of that era. Employed as professor of Natural Sciences at Haverford College, Cope was also curator of Herpetology at the Academy of Natural Sciences at Philadelphia (Adler 1989) and produced a series of papers describing new species from specimens in that collection and in other American east coast institutions. In one of these papers (Cope 1869), he described the brown gecko *Pentadactylus brunneus* from a specimen purportedly from Australia that had been sent to Philadelphia from the Paris collection. Despite the misleading locality, Cope correctly recognised its affinities to *Platydactylus duvaucelii*, considered to be an Indian species at the time. The species has recently (Nielsen et al. 2011) been resurrected from the synonymy of *Dactylocnemis pacificus*, following Hitchmough (1997), who discovered that it was closer to *Woodworthia maculata* than *D. pacificus*, with the distribution of the species including Banks Peninsula and Akaroa.

Akaroa was also the source of specimens for the last contribution of John Edward Gray to New Zealand herpetology, when he described the gecko *Naultinus lineatus* from a female and two young brought to him by Mr W. Adams (Gray 1869). Although Gray misspelt the name of the settlement as Otraroa, the error is excusable as he was suffering the effects of several strokes at this stage in life and was finding writing difficult (Gunther 1975). The mysterious Mr Adams is presumably William Adams, who advertised from Akaroa in a local newspaper on 20 May 1867 as being ‘lately from Lloyd’s, London … prepared to make up Average Statements, general and particular’ and offered ‘underwriting in all its branches’ (Adams 1867). He likely returned to London soon after. The brief article describing this species was overlooked for many years, and the type specimens are now unable to be found. Some have suggested that the name must refer to the only *Naultinus* found on the Banks Peninsula, in which case it antedates the name *Naultinus gemmeus* for this species (see Bauer and Henle 1994). Another possibility, given that the generic name *Naultinus* was applied by Gray in his earlier work to both brown and green geckos and that he did not in this instance indicate the general colour of his specimens, is that the name applies to one of the brown geckos from the region (R. Hitchmough, pers. comm.).

2.7 The Mysterious Kawekaweau

In 1986, Aaron Bauer and Tony Russell described a giant gecko, *Hoplodactylus delcourti*, the world’s largest, from a stuffed specimen found in the Museum d’Histoire Naturelle of Marseille. They noted a possible identification as the kawekaweau, a large lizard reported on several occasions from the North Island by the Māori during the first century of European settlement, an identification for which they subsequently provided additional evidence (Bauer and Russell 1987).

The species is likely to be extinct, and, unfortunately, there are no archival records of the early collections in Marseille to enable the source of the specimen to be identified, though the lack of a provenance implies that it preceded the earliest continuous records (which date from 1869). However, one might argue that if it is from New Zealand (see also alternative arguments in Worthy 2016), its location in a French museum means that it likely has come from one of the French expeditions or a French colonist.

In addition to Duperrey's visit to the Bay of Islands in 1824, Dumont d'Urville's surveys in New Zealand in 1827 and the French settlement at Akaroa (with de Belligny and other officials visiting North Island on several occasions to deal with the British officials; Buick 1928), there was one other French expedition in northern New Zealand waters in the first half of the nineteenth century that could have obtained the specimen.

Thirteen years after his previous visit, Dumont d'Urville returned with two ships, the *Astrolabe* again (like d'Urville, on its third visit to the southern hemisphere), this time accompanied by *La Zelée* (under the command of Charles Hector Jacquinot). The naturalists on this occasion were Jacques-Bernard Hombron (15.iv.1798–1852.x.16) and Honoré Jacquinot (1.viii.1815–1887.v.22), brother of the captain (Adler 2012). This expedition had as its main objective the exploration of the Southern Ocean and Antarctica and visited New Zealand between 26 March and 4 May 1840 (Dumont d'Urville 1846), again spending most of the time in the Bay of Islands. While the expedition report on this occasion did include an account of the reptiles collected, there are none mentioned from New Zealand.

Andrews (1986) noted that both the *Coquille* and the first *Astrolabe* expeditions returned to France via Marseille, where the natural history specimens were offloaded for transport to the Paris museum. He speculated that the kawekaweau specimen may have been secretly given to one of the expeditioners on the first *Astrolabe* voyage by William Williams (18.vii.1800–1878.ii.9), a medically trained missionary at Paihia who had arrived in the area less than a year before (Porter 1990), and sold when the expedition reached Marseille.

Other potential French sources for the holotype of *Hoplodactylus delcourti* resident in New Zealand during that era include the French Catholic missions that Bishop Jean Baptiste François Pompallier (11.xii.1801–1871.xii.21) established at various sites on the North Island in 1838–1845 (Simmons 1990) and the self-styled Baron Charles Philippe Hippolyte de Thierry (iv.1793–1864.vii.8), who resided in Hokianga and, later, Auckland in 1837–1850 and in 1853 until his death (Raeside 1990). Given the wide range of potential collectors and donors, it is unlikely that the mystery of the source of the mounted specimen will ever be solved.

2.8 The *Novara* Expedition and Ferdinand von Hochstetter (1857–1867)

The next scientific expedition to reach New Zealand departed from Austria. At the time, the Austrian Empire extended to the Adriatic Sea, and it was from the main port, Trieste, that the *Novara* Expedition set sail in 1857. This naval expedition, under the command of Commodore Bernhard von Wüllerstorf-Urbair, carried a team of scientists, headed by the zoologist Georg Ritter von Frauenfeld (3.vi.1807–1873.x.8), whose interests were primarily entomological. The *Novara* Expedition visited New Zealand between 22 December 1858 and 8 January 1859, mostly exploring around the Bay of Islands and Auckland. The *Novara's* visit coincided with the discovery of brown coal deposits at Drury, and the expedition was asked by both the New Zealand and New South Wales governments if it could spare its geologist, Christian Gottlieb Ferdinand von Hochstetter (30.iv.1829–1884.vii.18), to survey the new field and undertake additional geological explorations (Frauenfeld 1860; Scherzer 1862; Fleming 1990). Hochstetter remained in New Zealand until 2 October 1959, travelling extensively around both North and South Islands. His ten months in New Zealand formed the basis of his book, *Neuseeland* (von Hochstetter 1863).

Hochstetter's collections were treated as part of the *Novara* Expedition's legacy, which included about 20 lizard specimens from New Zealand, and, on return to Trieste, these specimens were studied initially by the ageing Leopold Joseph Franz Johann Fitzinger (13.iv.1802–1884.ix.20), who had previously (Fitzinger 1843) created the generic name *Hoplodactylus* for *duvaucelii*. Fitzinger (1860) published an initial report on the herpetological collections, but while some new names were proposed, there were no descriptions to validate the names. It was left to his successor at the Naturhistorisches Museum in Vienna, Franz Steindachner (11.xi.1834–1919.xii.10), to complete the work (Steindachner 1867).

In his report, Fitzinger listed five species of New Zealand gecko (*Hoplodactylus pacificus*, *H. grayi*, *H. elegans* and *H. punctatus*, all of which had previously been described as *Naultinus*, but which he now considered to represent his 1843 genus, *Hoplodactylus*, and one new genus and species, *Dactylocnemis Wüllerstorfii*). In addition, he listed three species of skink (*moco*, *smithii* and *ornata*, placing the first two species in the genus *Lampropholis* and the last in *Eulamprus*, both of which he had created in his earlier monograph for species from Australia; Fitzinger 1843). Steindachner (1867), in completing this work, continued to recognise the genus *Dactylocnemis* but identified Fitzinger's species *Wüllerstorfii* as *D. pacificus*. The lithographic illustration of the specimen was created by Eduard Konopičky (1841–1904; Adler 2014). Fitzinger's names were also used by von Hochstetter (1863), although he misspelt *Eulamprus* as *Eulampus*, creating another nomenclatural novelty.

2.9 The Rise of Science Within New Zealand (1870–1896)

The next contributions to New Zealand herpetology were from locally based naturalists, who were given the opportunity to publish their work by the establishment of the New Zealand Institute by Sir George Grey in 1867. This overarching body, which would later evolve into the Royal Society of New Zealand, represented a number of local scientific societies, jointly publishing their activities in the Institute's *Transactions*. The New Zealand Institute provided new connections between local collectors and resident scientists, facilitating rapid communication and transfer of specimens.

Sir Walter Lawry Buller (9.x.1838–1906.vii.19) (Fig. 2.4) was the first New Zealand-born naturalist to describe local lizard species. The son of a Wesleyan missionary, Buller, was appointed resident magistrate at Manawatu in 1862, aged just 24. However, his real passion was ornithology, and he obtained funding to travel to London in 1871 to arrange publication of his book on New Zealand birds. He returned to New Zealand in 1875 with a doctorate from the University of Tübingen and training in law, using the latter for employment as a barrister (Galbreath 1990).

On 22 October 1870, prior to leaving New Zealand for London, he presented his observations on the New Zealand lizard fauna to a meeting of the Wellington Philosophical Society in a paper published the following year (Buller 1871). In this, he described two new skinks, *Hinulia variegata* and *Mocoa striata*, and one new gecko, *Naultinus sulphureus*, the latter from Rotorua. Illustrations were provided by the New Zealand Institute's artist, John Buchanan (1819–1898). Buller's descriptions were scanty and largely limited to coloration, a feature possibly reflecting his ornithological paradigm. No locality data were provided for the skinks, and the name *Hinulia variegata* was unavailable, having already been used for a Philippine skink by Wilhelm Peters in Berlin in 1867. Buller commented that the first specimen of the gecko he had seen had been collected by Sir James Hector (16.iii.1834–1907.xi.6). Hector was a Scottish-born naturalist and geologist who had come to New Zealand after geological surveys in Canada to become director of the Geological Survey of Otago in 1861. He was, at the time, the only major scientist employed by the government (Dell 1990; Nathan 2015). Despite being primarily a geologist, Hector's biological interests were broad, and his administrative duties in science vast. These included directorship of the Colonial Museum, Wellington, and his role as manager of the New Zealand Institute. Hector not only supplied lizards to Buller, but he also sent some material to European collections, including a skink from the Chatham Islands that was later described by Wilhelm Peters in Berlin as *Lygosoma nigriplantare* (Peters 1873).

Buller continued to contribute to New Zealand herpetology after his return to New Zealand. In 1876, he described (Buller 1877) a new green gecko, *Naultinus pulcherrimus*, from two living specimens given to him by Arthur Samuel Atkinson (20.x.1833–1902.xii.10), a lawyer, naturalist and amateur astronomer of the New Zealand city of Nelson (Porter 1993). Atkinson had previously been a

Fig. 2.4 New Zealand resident authors and collectors of New Zealand lizards, 1870–1906: (**a**) Frederick Wollaston Hutton (Image: Alexander Turnbull Library, Wellington, MNZ-0474-1/4-F); (**b**) Sir Walter Lawry Buller (Image: Alexander Turnbull Library, Wellington, 1/4-004505-G); (**c**) William Colenso (Image: Alexander Turnbull Library, Wellington, 1/4-003097-F); (**d**) Henry Suter (Image: GNS Science, Lower Hutt, VML 166077)

journalist and politician in New Plymouth, but moved to Nelson in 1868. While Atkinson was the immediate source of the specimens used for the description, Buller had become aware of the species twice previously. Firstly, he had seen a note published in the *Transactions of the New Zealand Institute* (Anonymous 1874), reporting the exhibition at a meeting of the Nelson Association of a specimen collected by William Hunter (1835–1899.xi.15; station owner, prospector, sawyer and shopkeeper; Anonymous 1899a, 1906) from his property on the Upper

Matakitaki where he ran a store catering to the local gold rush. Secondly, Buller had been shown by Walter Mantell a preserved specimen and accompanying drawing (the latter made by a Miss Nairn) in the collection of the Colonial Museum.

Walter Baldock Durrant Mantell (11.iii.1820–1895.ix.7) was a key link in the scientific chain between New Zealand and England through his involvement in research on the moa. Born in Sussex, he was the second child of Dr Gideon Mantell, an enthusiastic amateur palaeontologist who played a critical part in the history of palaeontology as the discoverer of the dinosaur *Iguanodon*, a discovery that put Mantell Senior at odds with Richard Owen at the Royal College of Surgeons, who felt that dinosaurs (and moas) were his personal fiefdom (Cadbury 2000). Walter Mantell came to New Zealand in 1840, one of many who were persuaded to emigrate by the propaganda of the New Zealand Company. After a succession of positions in the local and regional government, and a return to England in 1855, he was elected to the New Zealand House of Representatives in 1861, later moving to the Legislative Council. Initially with his father as intermediary (seeking to build bridges with Owen), and later directly, Walter Mantell sent to Owen large amounts of moa material. His involvement with the Colonial Museum was sporadic, acting as curator during Hector's absences (Sorrenson 1990), and it was presumably during one of these periods that he showed Buller the specimen and drawing.

I have been unable to locate the drawing by Miss Nairn and am not sure of her identity, but she may have been Annie Nairn (b.1860), daughter of Francis Edward Nairn (1819–1910.xi.13), a sheep farmer, surveyor and artist of the Nelson area. Francis Nairn was appointed Royal Commissioner in 1879 to investigate a land purchase in South Island by Walter Mantell and had previously been surveyor on some of Mantell's expeditions. His wife, Betsy Wright Nairn, was also an artist.

In 1881, Buller described a new brown gecko, *Naultinus sylvestris*, from the Wanganui district, based on another live lizard given to him, this time by Joseph Robert Annabell (15.x.1857–1924.v.10) of the Survey Department. Annabell, born in Melbourne, had joined the survey department just a few years before and would have indulged his deep interests in ornithology as he explored the heavily forested and rugged area. He would later settle at Ngamatapouri (Godley 2007).

A few years later, in 1886, Buller retired and moved to London as Commissioner for the Colonial and Indian Exhibition. Returning to New Zealand in 1890, he bought a property at Horowhenua, which became the subject of a lengthy legal dispute. During this period, he contributed his last note on lizards, exhibiting a brown gecko at a meeting of the Wellington Philosophical Society on 16 October 1895 and commenting on its arboreality and capacity to change colour (Buller 1896). In this instance, the gecko was provided by Andrew Luff (1836–1920.ix.7) of Vogeltown, who is described in the electoral roll of 1896 as a settler of Pipitea and Murphy Street.

Buller moved to London for the third and final time in 1899, never again returning to New Zealand (Galbreath 1990).

The year after Buller's first paper on New Zealand lizards, another paper with similar scope appeared, written by Frederick Wollaston Hutton (16.xi.1836–1905.x.27). Hutton (Fig. 2.4) was the son of the vicar of Gate Burton, Lincolnshire in

England, and had some early training in applied science at King's College. He was commissioned as Ensign in the Royal Welsh Fusiliers and saw service in the Crimean War and the Indian War of 1857–1858, eventually rising to captain. An interest in geology acquired during his army service saw him appointed to the Geological Survey, initially in Waikato, and then Wellington and Otago, following his move to New Zealand in 1866 (Parton 1993).

Hutton's paper on the lizards of New Zealand (Hutton 1872) was, like Buller's, read before the Wellington Philosophical Society. The date, 16 September 1871, was after Buller's departure for London. Hutton used the paper to reexamine the specimens used by Buller (which have since been lost) as well as to examine other lizards in the collection of the Colonial Museum and noted some errors in Buller's paper. Hutton considered Buller's *Hinulia variegata* to be synonymous with *Mocoa zelandica* and described as new two more species of skink. One, *Mocoa laxa*, was later shown to be synonymous with *Oligosoma grande*; the other, *Norbea isolata* from White Island, represented the first New Zealand record of a genus otherwise known only from Borneo and suffered a similar fate to Hutton's *Mocoa laxa*, becoming a synonym of *Oligosoma smithii* (Hardy 1977), which Hutton had not seen. Hutton also described a new green gecko, *Naultinus elegans stellatus*, from a specimen collected by Jonathan Brough from the top of Mt Arthur. This specimen has since been lost, and a neotype in the Dominion Museum, Wellington, was nominated by McCann (1955), from Lake Rotoiti.

Jonathan Brough (1839–1927.i.31) was another of the group of amateur naturalists who were employed in positions that allowed them to explore their surrounds. Born in Cumberland in England, he came to New Zealand in 1867 after four years in Victoria, Australia, initially attracted to Australia by the gold rush but later exploring further afield in Gippsland, eastern Victoria. One of the first settlers in the Buller district in New Zealand, Brough was employed to construct roads in the region and later became an Inspector for the Roads Department (Anonymous 1927). He is commemorated by Brough Tabernacle on Mt Arthur, New Zealand.

In the year after his paper on New Zealand lizards, Hutton (1873) used the lizards as evidence for some biogeographic hypotheses on the origin of the New Zealand fauna in general—Hutton was an early disciple in New Zealand of Darwin's evolutionary theories.

Buller, living in London, would first have seen Hutton's paper after its publication in the Transactions and responded rapidly, his correspondence read at a meeting of the Wellington Philosophical Society of 20 July 1872. He noted that *Norbea* was unlikely to occur in New Zealand and rejected some of the 'corrections' made to his work by Hutton (Buller 1873). Such robust interactions between Buller, the amateur naturalist, and Hutton, the scientist, were repeated in their ornithological studies (Andrews 1986).

Hutton would later become curator of the Otago Museum, professor of Biology at Canterbury College and curator of the Canterbury Museum. His interests in the New Zealand fauna culminated in his monograph, *Index faunae Novae Zelandiae* (Hutton 1904), and the popular book, *The Animals of New Zealand* (Hutton and Drummond 1904), both summarising the lizard fauna. Sadly, he died at sea while returning to New Zealand after a visit to London, less than a year before Buller's death.

The third resident to name a lizard was William Colenso (17.xi.1811–1899.ii.10), one of the most well-known and controversial figures in nineteenth-century New Zealand natural history. Colenso (Fig. 2.4) was born in Penzance in Cornwall, the son of a saddler, and became apprenticed to a printer. This training drew him to New Zealand, where the Church Missionary Society in Paihia needed a local printer to produce their books and papers. Colenso arrived there at the end of 1834 aboard the *Blackbird*. One of his printing tasks was to produce a Māori version of the New Testament for William Williams, and this initiated an interest in Māori culture that was to last the rest of his life. While at the Bay of Islands, Colenso met many of the visiting naturalists, including Charles Darwin (1835), Allen Cunningham, the New South Wales Government Botanist (1838) and Joseph Hooker (1841), who came with the British Antarctic Expedition. Cunningham and Hooker saw in Colenso the potential for a local botanical collector, and Hooker, in particular, carefully cultivated his relationship with Colenso, encouraging Colenso's botanical activities as a collector while attempting to suppress his increasing appetite for the professional activity of describing species (Endersby 2008). Colenso took every opportunity to collect specimens during his extensive travels as part of his work for the church. In the early 1840s, Colenso began to train for ordination and married the daughter of another missionary, satisfying one of the requirements imposed by Bishop Selwyn. He was ordained Deacon in 1844 and sent to take over the mission at Hawke's Bay. However, he was suspended in 1852 when he was discovered having an affair with a young Māori member of his household. His wife subsequently left him, and for several years, he became a recluse, emerging in 1858 to enter politics, first as a local councillor and then nationally (representing Napier) until 1866, before becoming Inspector of Schools (Bagnall and Peterson 1948; Mackay 1990). With his experience with the Māori and his knowledge of natural history, he later eked out a career writing and collecting, with the *Transactions of the New Zealand Institute* giving him a local outlet independent of Hooker.

Colenso's entry into New Zealand lizards was a late move; his first paper on lizards (Colenso 1880) was read before the Hawke's Bay Philosophical Institute on 12 May 1879, when Colenso was 67 years of age. In it, he provided detailed observations on three living green geckos (one of which later gave birth) that were given to him by an unnamed source from Hampden. These observations extended over a period of 18 months and included extensive notes on behaviour, diet, sloughing and growth. Towards the end of these observations, he assigned the captive animals to a new species, *Naultinus pentagonalis*.

His next contribution (Colenso 1885) was read five years later, on 1 October 1884, at the Wellington Philosophical Society. Here, he described a brown gecko, *Naultinus versicolor*. He had collected two living individuals the previous year from Norsewood and, more recently, received a third individual from David Paton Balfour (12.vii.1841–1894.vii.1913) of Glenross. As with his first paper, he provided notes on the species in captivity.

Colenso (1887) returned to the Hawke's Bay Philosophical Institute on 9 August 1886 to read his final herpetological paper, once again dealing with observations on captive green geckos, this time based on a gravid female given to him by Mr J. Stewart in December. As this female produced two dead young at the beginning of winter, Colenso was able to confirm that the species was viviparous, with an extended gestation, an observation that was further confirmed by Balfour's observations on a captive female of *N. pentagonalis*. In his paper, Colenso was more circumspect in his identification of the gecko at hand, only being certain that it was not *N. punctatus*.

Balfour was a Scot who had come to New Zealand in 1862 to join the goldrush, but, meeting little success in this area, returned to an earlier career as a shepherd. Moving to Napier, he took over the lease of Kakariki station, unfortunately at a time of economic and social unrest. After taking on a succession of other station management positions, the 1880s depression saw him revert to working as a local council road inspector. Despite his humble range of jobs, Balfour was a learning enthusiast, accumulating an extensive library, and had particular interests in astronomy and botany (Brownlie 1993). It was via the latter interest and the Hawke's Bay Philosophical Institute that he was befriended by Colenso.

Like Balfour, John Stewart (sometimes John Joseph Stewart), the schoolmaster at Takapau School between 1880 and 1887 (and before that a teacher at Tamamu), was a country member of the Hawke's Bay Institute. He had a keen interest in natural history and exhibited specimens, particularly fossils, at the meetings on several occasions. I have not been able to locate his birth and death dates, but at the time of the termination of his teaching contract in 1887, he was described as old, though he remained in the Takapau region as a farmer for at least a short time.

Sadly, *Naultinus sylvestris* Buller and *Naultinus versicolor* Colenso were subsequently placed in the synonymy of *Hoplodactylus* (now *Mokopirirakau*) *granulatus* by Boulenger (1885) and McCann (1955), *N. pulcherrimus* Buller in the synonymy of *N. stellatus* Hutton by McCann (1955) and *N. sulphureus* Buller and *N. pentagonalis* Colenso in synonymy with *N. elegans elegans* and *N. elegans punctatus*, respectively, by Robb and Hitchmough (1980). Of the ten species and subspecies described by these local naturalists, only the skink *Oligosoma striatum* Buller and the gecko *Naultinus stellatus* Hutton are still recognised.

The fourth contributor to the local literature on lizard biology was Dr Frederick John Knox (3.iv.1794–1873.viii.5). Knox was the younger brother of the Scottish anatomist Robert Knox and assisted his brother in cataloguing his private museum. Unfortunately, Robert Knox was implicated in the infamous Burke and Hare affair whereby he received murdered victims for his anatomy teaching, and his career as a private anatomy teacher was ultimately ruined with the introduction of the Anatomy Act that followed Burke's execution. It was shortly after this, in 1840, that Frederick Knox came to New Zealand with his family and was immediately appointed as the librarian at the public library at Port Nicholson. When this was closed in 1842, he moved to Lower Hutt and returned to his former profession as a medical practitioner, obtaining various government medical appointments over time (Stephens 1968; Beasley 2001; Kaufman 2001). Upon his arrival in

New Zealand, Knox was entranced by the potential for anatomical studies of the fauna and began to write articles on the fauna for the local press (Parkinson 1983). His two papers on lizards, both dealing with caudal autotomy and regeneration in geckos, appeared in the *Transactions of the New Zealand Institute* in 1870 and 1873, near the end of his life. Knox was an anatomist, not a taxonomist, and the nomenclature he used for his study species has subsequently been shown to be incorrect. Knox's '*Naultinus greyii* Gray' (Knox 1870) is *Mokopirirakau granulatus* (Bauer and Henle 1994), and his '*Naultinus pacificus* Gray' (Knox 1873) is likely to be *Woodworthia maculatus*.

A hint of another paper on lizards, now lost, is provided by McCann (1955), who noted the existence of two lithographic prints by J. Buchanan in the collection of the Dominion Museum. These plates are now unable to be located (Whitaker and Thomas 1989). The second plate included two skinks with the otherwise unpublished names *Mocoa gilliesii* and *Mocoa gracilis*. John Buchanan, based in Wellington, was lithographer for the *Transactions of the New Zealand Institute*, and McCann (1955) indicated that the drawing of *Mocoa gilliesii* looked like *Oligosoma grande*. The lawyer, judge, politician and naturalist Thomas Bannatyne Gillies (17.i.1828–1889.vii.26), who had originally settled in the Otago area (within the range of *O. grande*) and later moved to Auckland, was the joint founder, with Hutton, of the Auckland Institute, and a frequent contributor to the *Transactions* with papers on mollusc shells (Rennie 1990). Given the connection with Hutton, and the fact that Hutton (1872) described two new skinks, one of them *Mocoa laxa*, a synonym *of O. grande*, it is possible that the Buchanan plates were prepared as illustrations to accompany Hutton's paper but not published when Hutton changed his mind on some of the names to use.

While resident naturalists were describing species during the 1880s, one specimen went elsewhere for description. In 1882, the zoologist Johann Gustav Fischer (1.iii.1819–1889.i.27), who was not only a teacher at a private school in Hamburg but also had a close association with Hamburg's Naturhistorischen Museum (Adler 2007), described a new genus and species of gecko, *Heteropholis rudis*, from an unspecified locality in New Zealand. His description was included in a paper describing several new reptiles from a variety of localities around the world (Fischer 1882) and was accompanied by an illustration by the Hamburg lithographer Eduard Ritter (1820–1892). The species, now in *Naultinus*, is restricted to the northeast part of South Island. Fischer (1882) listed the holotype as being in the collection of the Godeffroy Museum, but gave no collector. The Godeffroy Museum, at the time nearly insolvent, was a private museum that also operated as a dealership in natural history specimens (Bieler and Petit 2012). However, there are no documented collectors for the New Zealand specimens held by the museum (Panning 1956; Scheps 2005), and few of the specimens advertised for sale were from that country. Those that were, were mostly shells (during the 1860s) and birds (in the 1870s). It seems most likely that the holotype of *Heteropholis rudis* was obtained by Otto Finsch (8.viii.1839–1917.i.31), ornithologist, anthropologist and former director of the Übersee-Museum in Bremen (Sack 1972; Howes 2011) since the other species reported in Fischer's (1882) paper were part of the Bremen collection and Finsch had worked on the Godeffroy bird collections. Finsch had recently returned home after a four-year expedition to the Pacific (1879–1882), at the end of which he visited New Zealand. He arrived in New Zealand via the *Te Arua* from Melbourne, disembarking at Bluff on 23 May 1881, and left Lyttelton to head for Wellington aboard the *Wanaka* on 14 June (Anonymous 1881a, b, c). There would have been sufficient time for Finsch to have material he obtained on the South Island shipped home to Germany before Fischer's article was printed in November of that year (the printer's date at the foot of the article is November 1881, although the article was published in the April 1882 issue of the journal). The type specimen is now in the Natural History Museum in London (Bauer and Henle 1994).

2.10 The Boulengerian Era (1885–1906)

After this flourish of publications by local naturalists, attention returned to London with a series of publications by George Albert Boulenger (19.x.1858–1937.xi.23) of the British Museum (Natural History). Boulenger (Fig. 2.3), born in Brussels, came to the British Museum in 1881, aged 22, to take over responsibility for herpetology from Günther and was one of the most prolific herpetological authors of all time (Adler 1989). He began his work on the New Zealand lizards with a new *Catalogue of the Lizards in the British Museum* (Boulenger 1885, 1887). By this time, the British Museum collection had received additional specimens from several sources. Among these were a dozen from the Colonial Secretary, Dr Andrew Sinclair (13. iv.1794–1861.iii.26), who was also a botanical collector, like Colenso, for Joseph Hooker. Tragically, Sinclair's collecting was curtailed when he drowned at a river crossing while on an expedition with Julius von Haast, just three years after his return to New Zealand to collect for Hooker (Molloy 1990). Boulenger also had at hand ten specimens from an E.S. Ellisdon (possibly Edward Sallows Ellisdon, a pharmacist of Lyttelton in 1872, when Boulenger received his specimens, though he was later employed as a pharmacist at Dunedin), as well as material from three surveying expeditions. The first was the *Acheron* expedition of November 1848–May 1851, under the command of John Lort Stokes, who had also been aboard the *Beagle* with Darwin and had taken command of the *Beagle* for her subsequent surveying voyage to Australia; the surgeon/naturalists on this survey were David Lyall, 1.vi.1817–1895.iii.2, and Charles Forbes, 21.viii.1819–1886.v.21 (Hooker 1895; Hordern 1989; Natusch 1978; Wright-St Clair 2003). The second expedition was undertaken between September 1851 and Feb 1856 aboard the *Pandora*, under the command of Captain Byron Drury, 10.ii.1815–1888.xi.6, with John Joliffe, 5. i.1823–1891.ix.12, as surgeon and naturalist (Byrne 2007). The third expedition was conducted aboard the *Herald*, which visited the Auckland area between 7 and 22 June 1854 (David 1995) under the command of Henry Mangles Denham (28. viii.1800–1887.vii.3), with John MacGillivray (18.xii.1821–1867.vi.6; Calaby 1967) as naturalist. Specimens from these three expeditions were presented by

Stokes, Drury and MacGillivray, respectively. Boulenger also received specimens from the *Challenger* expedition, which visited Wellington between 28 June and 6 July 1874 (Tizard et al. 1885). The British Museum had been sent the holotype of Hutton's *Norbea isolata* and a specimen 'typical' of his *Lygosoma laxa* by the Colonial Museum (the latter may be the actual holotype of *laxa*, which is now unable to be found in the collection of the Museum of New Zealand Te Papa Tongarewa, the successor to the Colonial Museum and Dominion Museum).

Most of this additional material was just used to provide new and expanded descriptions of the known species, with some new synonymies. However, one specimen proved both interesting and problematic. Boulenger (1887) described a new species, *Lygosoma infrapunctatum*, from a single specimen received in 1863 from Gerard Krefft, curator of the Australian Museum (the original registration number on the specimen, 63.6.16.12, indicates registration on 16 June 1863). The specimen was given the locality Australia, but it has since been recognised as a New Zealand species (McCann 1955). Of the 102 specimens that were registered from Krefft on that day, most have no locality in the accession book, but appear with the locality Australia in the catalogues. A minority of specimens do have localities, and these include Queensland, New South Wales, Sydney, Cooks River, Clarence River and Melbourne. I presume that Krefft did not provide localities for the majority of the collection he sent on that occasion and that the British Museum simply gave such specimens the locality Australia by default. Johann Gerhard Louis Krefft (17.ii.1830–1881.ii.19), known in Australia as Gerard Krefft, was born in Brunswick, Germany, and first came to Australia in 1852 to join the Victorian gold rush. For a short period (1857), he was employed as a collector and artist for the National Museum of Victoria before returning to Germany in 1858–1859 (Adler 1989). In 1860, he came out to Sydney and was appointed assistant curator to the Australian Museum under Simon Rood Pittard and was temporarily appointed acting curator following Pittard's death on 19 August 1861. Krefft was not formally appointed as curator until the end of 1862, following a dispute between the Museum Trustees and the New South Wales Government (Anonymous 1862). It is important to note that the specimens received by the British Museum from Krefft in 1863 were purchased from him, rather than being received by donation or exchange from the Australian Museum. Hence, Krefft may have been selling his own personal collection rather than sending material from the museum's collection. Although the Australian Museum did have New Zealand reptiles in the collection at the time, having received some from James West Stack (27.iii.1835–1919.x.13) in April 1857 (Anonymous 1857), this donation is not likely to be the source of the type of *Lygosoma infrapunctatum*, as Stack was at the time teaching in the Auckland area (Murray 1990), too far north for this species, although he could have received specimens from further afield.

Some of Boulenger's lizard descriptions were illustrated by plates, the work of Pierre Jacques Smit (1863–1960) in the case of the New Zealand gecko plates and Robert Mintern (1840–1908) for the New Zealand skink plates. Smit and Mintern were part of a team of British Museum artists who prepared plates for Boulenger's catalogue (Adler 2014).

Boulenger's work provided the framework for the next contribution, by two Australian herpetologists: Arthur Henry Shakespeare Lucas (7.v.1853–1936.vi.10) and Charles Philip Frost (11.viii.1853–1915.ix.18). Lucas, a schoolteacher with professional zoological training from England, and at the time headmaster of Newington College in Sydney, had been working with Frost, an amateur naturalist in Melbourne (Shea 2004; Adler 2012), studying the herpetofauna of Victoria. It had become necessary for them to explore the potential for relationships between the southeastern Australian lizards and those of New Zealand (Lucas and Frost 1897). Hence, with the assistance of collections loaned to them by Hutton and others, they familiarised themselves with the fauna and came to the same conclusions as Boulenger. Their study represents a synthesis of Boulenger's descriptions with their own observations, as well as those of Hutton, Buller and Colenso.

In 1893, another Victorian zoologist, Arthur Dendy (20.i.1865–1925.iii.24), moved to New Zealand to take up a position as lecturer in biology at Canterbury College. One year later, he had been promoted to professor, replacing Hutton (who had become curator at the Canterbury Museum). In Victoria, Dendy had been at the University of Melbourne under Walter Baldwin Spencer and, together with Spencer, Lucas and Frost, had worked on the charismatic peripatus and planarian worms there. On moving to Canterbury, he retained these interests but added research on the tuatara to them (McLachlan 1935; Godley 1998). With his broad zoological interests, he exhibited lizards at meetings of the Philosophical Institute of Canterbury, commenting on reproduction and systematics (Anonymous 1899b). In 1901, he exhibited some skinks from the Pitt Island in the Chatham group (Anonymous 1901) and sent two of them to the British Museum. Boulenger (1902), overlooking the prior description of skinks from the same island group as *Lygosoma nigriplantare* by Peters (1873), named Dendy's specimens after their collector, as *Lygosoma dendyi*.

Four years later, Boulenger (1906) received additional skinks from New Zealand islands, this time from Henry Suter (9.iii.1841–1918.vii.31). Suter (Fig. 2.4), born in Switzerland, trained as an analytical chemist and came to New Zealand in 1887, where he was best known as a malacologist (one who studies molluscs), working with both extant and fossil faunas (Beu 1996). Boulenger recognised two species among Suter's collections, which he named *Lygosoma suteri* and *Lygosoma homalonotum* (the plate accompanying the description was by James Green, 1859–1936; Adler 2014). Although Boulenger noted at the time that the specimens were on loan to him, they were registered into the British Museum collection in March 1907. The localities given for the two species by Boulenger were Great Barrier Island and Flat Island, respectively. However, this has proven problematic for later workers since *Oligosoma suteri* is now known to occur on many of the islands around North Island whereas *O. homalonotum* is restricted to Great Barrier Island, and it has been proposed that the labels on the types were inadvertently swapped around or the localities otherwise confused (McCann 1955; Hardy 1977; McCallum 1980).

Two other taxonomic papers dealing with New Zealand lizards appeared at the beginning of the twentieth century. The first of these was by Samuel Walton

Garman (5.vi.1843–1927.ix.30), assistant in charge of Herpetology and Ichthyology at the Museum of Comparative Zoology at Harvard University. Garman (Fig. 2.3) had been brought from California in 1872 by Louis Agassiz, the Museum's founder (Adler 1989). Louis' son, Alexander Agassiz, who took over from his father as curator of the Museum, made several expeditions to the Pacific (to the Great Barrier Reef in 1896 and to the South Pacific in 1897–1898 and 1899–1900; Stephens and Calder 2006). On all of these trips, Agassiz was assisted by William McMichael Woodworth and Alfred Goldsborough Mayer, his two assistants in marine zoology. The herpetological collections made during these voyages were received by Garman, who reported on them in 1901 (Garman 1901), with illustrations by James Henry Blake (1845–1941; Adler 2012). Among the species in that paper, Garman described a new gecko, *Woodworthia digitata* (Garman spelt the species name *digatata* in the description, but *digitata* on the accompanying plate—most subsequent authors have used the second spelling as correct). Unlike the other specimens reported by Garman (1901), the two syntypes of *Woodworthia digitata* were not collected by any of the participants on the voyages or collectors they met during the expeditions. Instead, the *Woodworthia* types were much older specimens in the museum collection, obtained by 'Mr Edwards' from New Zealand. This was Henry Edwards (viii.1827–1891.vi.9), an English actor and naturalist with a particular interest in entomology (Brown-May and May 1997), who, after several years treading the boards and managing theatres in Victoria, Australia, travelled to New Zealand in February 1865 (Anonymous 1865a). Settling in Auckland, Edwards managed the Prince of Wales Theatre there and acted in many of the productions before leaving New Zealand for Peru on 30 April 1866 (Anonymous 1866). While in New Zealand, Edwards seems to have spent most of his time in Auckland, apart from a tour to Nelson and Hokitika with the Christy's Minstrels in October (Anonymous 1865b). After Central and South America, Edwards settled in San Francisco (1866–1878), running theatre companies there, and worked extensively on the Lepidoptera collection at the Californian Academy of Science before moving to the east coast, settling in Boston (1878–1880) and later, New York (1880–1891).

The eponymous Woodworth (viii.1864–1912.v.28) was assistant in charge of Vermes (worms) as well as Agassiz' personal assistant in the running of the museum and a controversial figure in Boston of that era. On the one hand, he was a flamboyant member of Boston society (Kline 1912; Shand-Tucci 2003; Austen and Crowley 1991), but to Meyer and his colleagues, he was lazy and repellent in his sycophancy to Agassiz (Stephens and Calder 2006; Winsor 1991). The species name remains in synonymy (Bauer and Henle 1994), but the generic name has recently been resurrected for the brown gecko genus containing *maculatus* (Nielsen et al. 2011).

The other contribution to New Zealand lizard systematics from this period came from the Austrian zoologist Franz Joseph Maria Werner (15.viii.1867–1939.ii.28). Despite being one of the preeminent Austrian herpetologists of his era, Werner was actively excluded from working with the collection of the Naturhistorisches Museum in Vienna by the then director, Franz Steindachner, possibly through jealousy. Instead, he forged a career working with collections in other parts of Europe while employed at the University of Vienna (Adler 1989). In a short paper, Werner (1895) described as new a skink, *Lygosoma* (*Leiolopisma*) *micans*, from a specimen in the University collection. No collector was provided in the description, and the species is now considered synonymous with *Oligosoma aeneum* (Hardy 1977). The type has been transferred to the Naturhistorisches Museum in Vienna (Tiedemann et al. 1994).

The likely source of this specimen was the infamous Austrian natural history collector Andreas Reischek (15.ix.1845–1902.iv.3). Initially apprenticed to a baker, Reischek was a keen naturalist and taxidermist. When von Hochstetter (by then director of the Natural History Museum in Vienna) was asked by Julius von Haast at the Canterbury Museum for a recommendation for a taxidermist, von Haast (who knew of Reischek through Steindachner) recommended him. Reischek arrived at Dunedin aboard the *Tangaroa* on 20 April 1877 and spent the next two years mounting specimens in Canterbury before commencing a decade of collecting zoological and ethnological specimens (including looting cave burial sites and Māori artefacts). He collected in the Canterbury area and then extensively in Northland, the King Country and the Fiordland sounds. On his return to Austria in April 1889, he brought with him some 16,000 specimens, of which about half were reportedly fish and reptiles. While much of his collection was sold to the Naturhistorisches Museum in Vienna, some was dispersed to other Austrian collections (King 1981). Those sold to the Vienna Museum were examined by Steindachner, who attached manuscript names to some of them (Bauer 1987), although these were never published.

Six years later, Werner (1901) contributed a second paper on New Zealand lizards, describing the New Zealand material held as part of a collection of Pacific reptiles made by the German zoologist Hugo Hermann Schauinsland (30.v.1857–1937.vi.5), one of Finsch's successors at Bremen. Schauinsland's New Zealand collections are mainly from Cook's Strait and the Chatham Islands (Dawson and Dawson 1958), although the herpetological collections also include a couple of specimens from localities on South Island. Although no new species were described from this material, new data on three gecko species and two skink species were provided. He also spelt *Naultinus* as *Naulthinus*, though it is not known if this was intentional or a typographic error.

2.11 A Hiatus in Research (1907–1956)

Boulenger's (1906) description of the two species *Lygosoma suteri* and *L. homalonotum* ended a lengthy period of research that was mostly taxonomic in nature. For the next half a century, research on the New Zealand lizard fauna was largely nonexistent. What little work did appear was largely on lizard parasites (Doré 1919; Percival 1941; Womersley 1941; Dumbleton 1947; Laird 1949, 1951), together with a series of anatomical studies by Mary Mackay Macdonald Boyd

(1934, 1935, 1939, 1940, 1942), Thomas Emmanuel Woodward (1941), John Gordon Buchanan (1956), Neville and Elsie (Pat) Stephenson (Stephenson 1939, 1948, 1960; Stephenson and Stephenson 1956) and Neville's student, Lyn Holder (Holder 1960). This period ended with the transfer of the Stephensons to Sydney (to the University of Sydney and University of New South Wales, respectively; Shea 2015) and with a new taxonomic revision of the New Zealand lizard fauna by McCann (1955), the last attempt at a taxonomic study of the entire lizard fauna.

Yule Mervyn Charles McCann (4.xii.1899–1980.xi.29) (Fig. 2.5) was born at Castle Rock, on the border of Goa, India. Following an initial period as a laboratory assistant at St Xavier's College in Bombay, he joined the Bombay Natural History Society in 1921, first as a field collector and eventually becoming assistant curator. His interests in natural history were wide-ranging, beginning with work on grasses. With the independence of India, he migrated to New Zealand in 1947, bringing with him a large preserved collection of Indian reptiles and amphibians (Gill and Froggatt 2014), and was employed by the Dominion Museum in Wellington. Almost immediately, he began working on the New Zealand lizard fauna (McCann (1955) notes receipt of living specimens collected in 1948), producing his monograph eight years after arriving in the country. McCann retired from the Dominion Museum in 1964 and took up a position at the New Zealand Oceanographic Institute, which ended in 1969. At the age of 70, he began working as a garage mechanic to make ends meet (Adler 1989).

McCann's lizard monograph was a new platform for the study of the local fauna, providing the first thorough redescriptions of the existing species since Boulenger (1885, 1887) and Lucas and Frost (1897). This time, the descriptions were primarily based on the available material in local museums rather than on small samples of faded material with poor locality data in European collections. However, like the previous studies, McCann's monograph suffered from limited sampling of many species as the local museums were still relatively poor in their lizard collections from many regions. Further, McCann was, for the most part, unable to directly examine the type specimens in European collections, relying instead on measurements and scale counts provided by those museums. Despite this, in this one paper, McCann recognised four new geckos and eight new skinks, the largest single increase in the New Zealand herpetofauna. The four new geckos were all from the South Island, and all were placed in the genus *Heteropholis*. Three of these were green geckos, now placed in *Naultinus, gemmeus*, *manukanus* and *tuberculatus*, and one, though originally placed with the green geckos, is a brown gecko, later placed in *Hoplodactylus* and now in the genus *Mokopirirakau*: *nebulosus*.

McCann was assisted in his studies of the New Zealand geckos by the availability of live material. The description of *Heteropholis manukanus* was based primarily on a live individual from the Marlborough Sounds presented to the Dominion Museum in 1948 by a Miss Gibbons. *Heteropholis gemmeus* was similarly based largely on a live female and her two young, collected by Drury (no further details provided) from Rangiora and sent to McCann by the Canterbury Museum. While the holotype of *H. manukanus* was preserved and is still held in the Museum of New Zealand Te Papa Tongarewa, the holotype and two juveniles of *H. gemmeus*

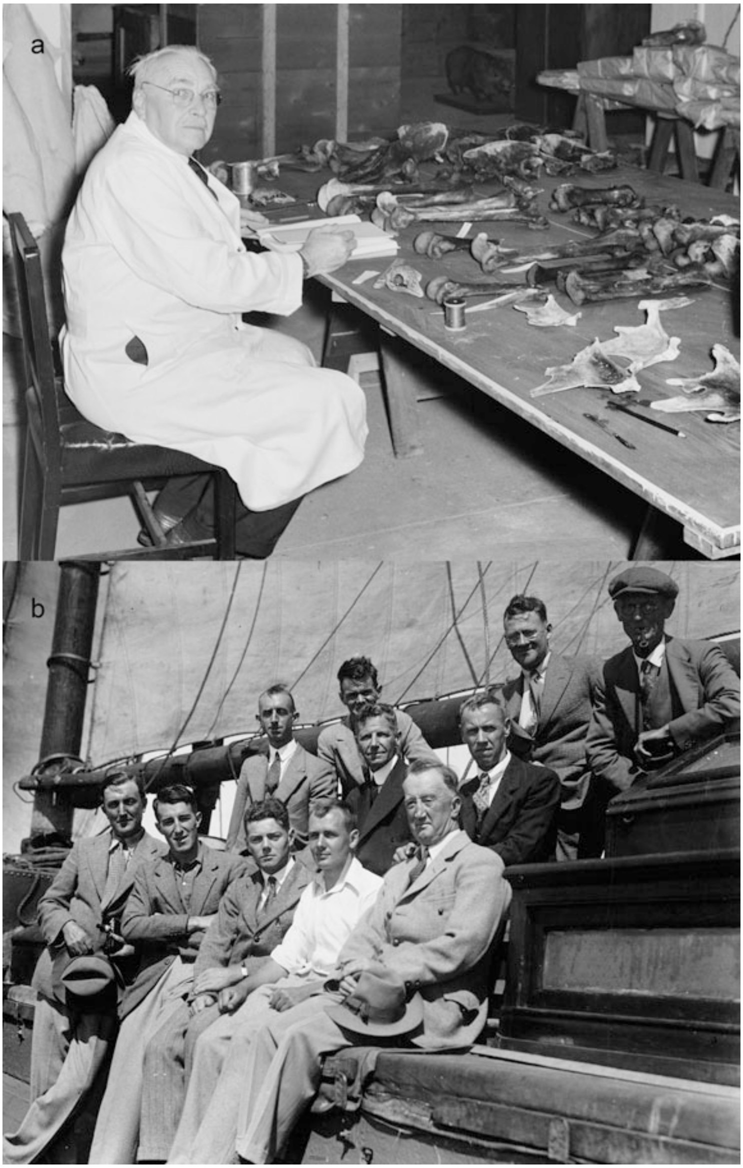


Fig. 2.5 (**a**) Yule Mervyn Charles McCann, working with moa bones (Image: Museum of New Zealand Te Papa Tongarewa, MA1245817). (**b**) The members of the *Will Watch* expedition, 1935: *left to right*, *front row*: George Middleton Turner (1893–1973), Evan Graham Turbott (1914–2014), Charles Alexander Fleming (1916–1987), Geoffrey Thomas Sandford Baylis (1913–2003), Dr William Aiken Fairclough (1881–1968). *Second row*, *left to right*: Richard Seymour Fletcher (1899–1988), Harrie Archdall Adams (1878–1960), Walter Reginald Brook Oliver (1883–1957). *Third row*, *left to right*: Robert Alexander Falla (1901–1979), Arthur William Baden Powell (1901–1987), Professor John Arthur Bartrum (1885–1949). (Image: Alexander Turnbull Library, Wellington, PAColl-3259)

seem to have been lost, unable to be found by Freeman and Tunnicliff (1997) at the Canterbury Museum. I have been unable to further identify Miss Gibbons or which of the numerous Drurys in the Canterbury area in that era was responsible for collecting these specimens. The third gecko species, *H. tuberculatus*, was based on a holotype with no recorded collector and only the locality Westland.

The discovery of the brown gecko *Heteropholis nebulosus* was due to the efforts of the ornithologist Edgar Fraser Stead (22.x.1881–1949.ii.7). Stead, born in Christchurch and trained as an electrical engineer, but with an inheritance that enabled him to concentrate on his passions (which, in addition to field ornithology, included breeding rhododendrons and azaleas on his property in Christchurch), combined a long-term interest in Stewart Island and its surrounding islets with wildlife photography, particularly of birds on their nests (Wilson 1949; Turbott 1998). It was while on his only visit to Cundy Island (now Kundy I.) between 12 November and 4 December 1929 (Miskelly 2012) that he collected the holotype of *Heteropholis nebulosus* 'in a bird's nest about thirteen feet from the ground' (McCann 1955).

Among the skinks, McCann found much geographic and local variation in coloration and scalation, but much of this was subtle, and many of his new taxa were described as subspecies. Within *Leiolopisma grande*, he added the subspecies *otagense*, with a specimen collected from Otago by a Mr Acland as the holotype, and the subspecies *waimatense*, with its holotype collected by R.W. Wilson in January 1925 from Waimate. These have subsequently been raised to full species. Although McCann did not provide further details of Acland (who he spelt as Ackland), it is likely to be either John Barton Arundel Acland (1823–1904), who founded Mt Peel Station, his nephew Thomas Dyke Acland (3.vii.1846–1892), a merchant and land agent in Christchurch or one of their descendants.

The Dominion Museum herpetology collection was heavily skewed towards material from offshore islands, much of it collected by ornithologists and malacologists, several of them colleagues of McCann. From the northern island groups, the Poor Knights and the Three Kings, McCann described the species *Leiolopisma fallai* and *L. oliveri*, the types of both collected by Walter Reginald Brook Oliver (7.ix.1883–1957.v.16). Oliver (Fig. 2.5), who developed a keen interest in natural history as a child, was born in Tasmania, but came to New Zealand with his parents in 1896. Initially employed by the Customs Department, he was moved from city to city, and in 1907, he was posted to Timaru, where he met the local naturalist Walter Lawrence Wallace. Together, they planned an expedition to the Kermadec Islands in 1907–1908. This whetted his appetite for the natural history of islands, and spurred by subsequent moves around the country by the Customs Department, he visited the Chatham Islands (1909), Stewart Island (1910) and the islands in Hauraki Gulf (1912). Following service in the First World War, he used the period of demobilisation to spend some time visiting botanical collections at Kew and the British Museum (Natural History) in the United Kingdom before returning to New Zealand. In the early 1920s, he was appointed senior scientific assistant at the Dominion Museum and became director in 1928 with the death of the previous incumbent. His appointment as director coincided with major changes, with a combination of the economic problems of the depression and a new museum building occupying much of his time over the next decade (Dell 1998a). However, despite his administrative duties, he was able to find time to participate (along with Robert Falla and Graham Turbott) in the *Will Watch* expedition of February 1934 (Matthews 1988), during which he collected the types of the two skinks. Oliver's woes continued with the start of the Second World War, which resulted in the closure of the museum to the public between 1942 and 1949. Together with the funding cuts and the loss of staff, this further hampered his work. He retired from the Dominion Museum in 1947, but for a short period was temporary director of the Canterbury Museum (1948). It was while he was here that he sent McCann the live holotype of the gecko *Heteropholis gemmeus* and its two offspring.

Robert Alexander Falla (21.vii.1901–1979.ii.24) was Oliver's successor as director of the Dominion Museum, occupying this role while McCann was there. He was also a participant in the *Will Watch* expedition to the northern islands (Fig. 2.5) during which the types of *oliveri* and *fallai* were collected. Falla was born in Palmerston North, New Zealand, and at an early stage fell in love with the sea. While his degrees were in education, his interests in natural history, whetted by a short time aboard the *Dana* expedition in 1929, were enough to gain him an honorary position with the Auckland Museum. Later that year, he participated in Sir Douglas Mawson's British, Australian, New Zealand Antarctic Research Expedition (BANZARE) to Antarctica and the subantarctic islands and in 1931 was appointed ornithologist and education officer at the museum, followed by promotion to assistant director in 1937. At the Dominion Museum, he initially became mired in the same wartime financial and staffing issues that Oliver had experienced, but he was able to see these through and set the museum back on a research track, encouraging fieldwork, before his retirement in 1966 (Dell 1998b).

While these first four species and subspecies of skink (*otagense*, *waimatense*, *oliveri* and *fallai*) are still recognised (all now considered full species), McCann's other species and subspecies have since been placed in synonymy.

He was, like others before him, confused about the identity of the skinks from the Chatham Islands and named *Leiolopisma turbotti* from a series of specimens collected from The Pyramid, in the Chatham group, by Evan Graham Turbott (27.v.1914–2014.xii.12), another ornithologist. Born in Auckland, Turbott (Fig. 2.5) was educated at the University of Auckland, where he completed his MSc degree on the anatomy of the frog *Leiopelma hochstetteri*. He was employed in 1937 as assistant zoologist at the Auckland Institute and Museum, where he would succeed Robert Falla as ornithologist. During the war, he was posted to the Auckland Islands, taking the opportunity to study the local fauna while coastwatching. Between 1957 and 1963, he was assistant director at the Canterbury Museum before returning to the Auckland Institute and Museum as director (Gill 2014). Like Oliver and Falla, he had a particular interest in the ornithology of New Zealand's islands, and his visit to the Chatham Islands in 1937–1938, accompanying Charles Fleming, and during which he collected the types of his eponymous skink, was his second offshore expedition after the *Will Watch* expedition.

McCann also had access to skink samples from many of the Cook Strait islands and named *Leiolopisma festivum* from The Brothers. Unfortunately, he overlooked an earlier use of that name for a New Caledonian skink, and McCann's *festivum* can no longer be used. Hardy (1977) analysed patterns of geographic variation within *Oligosoma lineoocellatum* using larger and more geographically representative samples and found that the populations distinguished as *festivum* were part of a more general pattern of variation, placing McCann's species in synonymy with *O. lineoocellatum*.

The type series of McCann's *festivum* was collected by the malacologist Richard Kenneth (Dick) Dell (11.vii.1920–2002.iii.6), who is also listed by McCann as collector of many of the lizard specimens from the Cook Strait islands. Dell was a shell collector from an early age and volunteered to work with the malacology collection at the Auckland Museum. Following the war, he was offered a job as conchologist (one who studies shells) at the Dominion Museum and would eventually become assistant director under Falla (1961) and then Falla's replacement as director (Beu et al. 2003).

McCann's new subspecies *Leiolopisma smithi numerale*, from the islands at the southern end of the distribution of this species, would suffer a similar fate to his *Leiolopisma festivum*. The types of this subspecies were collected by another naturalist with an interest in islands, Bernard Sladden (28.x.1879–1961.v.25), from an island named after him, Sladden Island, near Great Mercury Island (although the name is no longer used). Sladden began his career as a farmer and cattleman, developing an interest in wildlife from his time working on the land. After the First World War, he was appointed honorary ranger for Motuotau Island and then in 1932 became inspector with responsibility for all islands in the Bay of Plenty, a position that allowed him to enjoy his interest in the sea and the history of New Zealand marine exploration (Rorke 2000).

The one skink McCann named from the North Island mainland, *Leiolopisma latilinearum*, has also been placed in synonymy (Hardy 1977), this time with one of Buller's species, *Hinulia striata*. In the absence of a type specimen for Buller's *striata*, McCann felt that it was not possible to determine what species was involved. However, Hardy (1977) demonstrated that the illustration provided by Buller for his species was clearly that represented by McCann's *latilinearum*. McCann described *latilinearum* from a holotype in the Whanganui Museum, collected by a H. Grubner from Kakahi on North Island, and one other specimen purportedly from Wellington, a locality from which the species is not otherwise known (Hardy 1977). Grubner was almost certainly Herbert Ellis Grubner (3.iv.1908–1996.v.4), who was on the 1940 World War 2 ballot list as a dairy farmer from Kakahi.

McCann's final nomenclatural change reflected his inability to examine type specimens of skinks in the British Museum. Confused by the inconsistencies in some of Gray's early descriptions, McCann considered that the Gray's name *Tiliqua ornata* was applicable to *L. zelandicum* and not to the species to which the name *ornatum* had been applied for a century, which in McCann's view was now unnamed. He gave it the name *Leiolopisma pseudornatus*. Unfortunately, McCann was wrong about the identity of the type, and *ornatus* has been returned to the species to which it had been previously applied, with *pseudornatus* as its synonym (Hardy 1977). Curiously, it was recently discovered that McCann was correct in principle, with the original holotype of Gray’s *Tiliqua ornata* not representing the species that bore that name subsequently (though also not the species McCann thought it was)—this issue was resolved, maintaining majority usage, through designation of a neotype by Hitchmough and Patterson (2010, 2011).

2.12 A New Start (1956–1969)

The next phase of studies on the New Zealand lizard fauna began in the late 1950s and early 1960s and emphasised physiology and its application to ecology, particularly the adaptations of lizards to New Zealand’s cold climates. Prime among these was the first detailed study of the ecology of any New Zealand lizard, the common skink of the Wellington region (then identified as *Leiolopisma zelandica*), conducted by Richard Essex Barwick (Barwick 1955, 1959). This was followed by a similarly detailed study by James Davidson Fawcett on *Oligosoma ornatum* (as *Sphenomorphus pseudornatus*) in the northern part of North Island (Fawcett 1964a, b, 1970). New collections were made, and field workers began to experience difficulties in using McCann’s taxonomy to identify the lizards they found, suggesting that more work on lizard taxonomy was needed, despite the previous one and a half century’s research on the topic and McCann’s herculean efforts. The days of researchers having broad research programmes covering the full spectrum of New Zealand’s lizard fauna had ended, and from this time to the modern day, research on skinks and geckos has been undertaken by different groups of researchers.

2.13 The Modern Era of Skink Systematics (1970–)

The modern era of skink systematics began with a series of descriptions of new species by Joan Robb (b. 11.xii.1921) of the University of Auckland, who described *Leiolopisma alani*, *L. pachysomaticum* and *L. macgregori* (Robb 1970, 1975) from offshore islands, beginning to apply genetic evidence to the issue of species delineation by using allozyme electrophoresis (Robb 1975). Robb also began the process of resolving nomenclatural issues with some of Gray’s early descriptions by reexamining the original type specimens (Robb 1977).

Leiolopisma alani was named by Robb after her nephew (Gill and Whitaker 1996), although the holotype (Gill 1983) was collected by Asa Clifford Thoresen (9.ix.1930–2006.iii.31) of Andrews College, Michigan, on one of his return trips to his New Zealand homeland.

Leiolopisma macgregori was named for William Roy McGregor (8.vii.1894–1977.vi.1), known irreverently as ‘Barney’, the inaugural lecturer in charge of the Zoology Department at the University of Auckland and Robb's mentor. McGregor created the University's Museum of Zoology, founded the New Zealand Conservation Society and was instrumental in gaining support for reservation of the Waipoua kauri forest (Morton 1998).

New Zealand skink systematics began to incorporate a more field-based approach when Brian James Gill, a student at Massey University, looked at the comparative ecology of some of the superficially similar small brown skinks for his honours thesis (Gill 1975), a study that was published a year later (Gill 1976). Gill's work emphasised ecological differences between the species, which corresponded to morphological and colouration differences. At the same time, Graham Stuart Hardy (b. 25.iv.1947) at the Victoria University of Wellington was working on the systematics of the skink fauna using morphology, karyotypes and the new technique of allozyme electrophoresis (Hardy 1976, 1977, 1979, 1982; Hardy and Hicks 1980). He identified a number of new species: *Cyclodina whitakeri*, *Leiolopisma acrinasum* and *L. chloronoton* were described from new samples from remote areas, and a new subspecies, *L. nigriplantare maccani*, was described for mainland populations of that species, while *Leiolopisma gracilicorpus* was more controversially described from a single old faded specimen in the collection of the Auckland Institute and Museum (Hardy 1977). This became something of a mystery for several decades afterwards (Gill (1983) identified the collector as a Mr Webster, but was unable to identify which of several Websters resident in Hokianga had collected the specimen). The species has most recently been synonymised with *O. homalonotum* (Chapple et al. 2009). Hardy's taxonomic conclusions for some of the more wide-ranging species were significantly different to those of McCann (1955) and Robb (1975), and some of their subspecies and species were placed in synonymy with other species, including Robb's only recently described *Leiolopisma pachysomaticum*.

With this new taxonomic baseline to work from, Geoff Patterson at the University of Otago began a doctoral study looking intensively at Hardy's *Leiolopisma nigriplantare maccanni* in the Otago region (Patterson 1985a, b), a subspecies that Hardy had found to be extraordinarily variable. Patterson found, as with Gill's studies of small brown skinks on the North Island, that there were consistent morphological and ecological differences between colour forms within what had previously been considered a single subspecies and that some of these forms were electrophoretically distinguishable, retaining their genetic differences in sympatry with each other. This work was later extended (Daugherty et al. 1990), resulting in the partitioning of *maccanni* into three species, *Oligosoma inconspicuum*, *O. notosaurus* and *O. maccanni*, with a residue of populations (though still covering an extensive range) left as a new subspecies of *O. nigriplantare*, *O. n. polychroma* (Patterson and Daugherty 1990). *Oligosoma inconspicuum*, when further studied two decades later, was also revealed to be a complex of species (Chapple et al. 2011).

The recognition of multiple new species in these taxa led to similar studies using a combination of genetic and morphological analyses on other species that showed geographic variation in morphology in earlier studies. This resulted in the recognition of additional new and resurrected taxa in the *O. grande* complex (Patterson 1997), *O. aeneum* (Chapple et al. 2008a), *O. oliveri* (Chapple et al. 2008b) and *O. ornatum* (Patterson et al. 2013). In addition to this synthetic and analytical work, additional distinctive species with restricted ranges have continued to be discovered and described as new collections have been made, often from remote areas (Patterson and Daugherty 1990, 1994; Chapple and Patterson 2007; Bell and Patterson 2008; Patterson and Bell 2009).

2.14 The Modern Era of Gecko Systematics (1980–)

In contrast to the recent explosion of work on the alpha taxonomy of New Zealand skinks, equivalent work on the New Zealand gecko fauna has been much slower to appear, despite evidence for the existence of many new cryptic species.

After completing her work on the New Zealand skinks, Joan Robb began to work on the geckos, first (Robb 1980) describing three new species, *Hoplodactylus chrysosireticus*, *H. stephensi* and *Heteropholis poecilochlorus*, and then collaborating with others to separate *Hoplodactylus maculatus* from *H. pacificus* (Robb and Rowlands 1977) and revise *Naultinus* on the North Island (Robb and Hitchmough 1980). Very distinctive new species of brown geckos were described by Bruce Thomas (1981: *Hoplodactylus rakiurae* from Stewart Island) and Tony Whitaker (1984: *Hoplodactylus kahutarae* from high altitudes in the Seaward Kaikoura Range). However, the taxonomy of the remaining species has been subject to a variety of different opinions (see, e.g., the conflicts between the various papers in a symposium on New Zealand herpetology held at the Victoria University of Wellington in 1980; Newman 1982).

Genetic techniques began to be applied to these controversies by Rodney Arthur Hitchmough (1997) in his PhD thesis at Victoria University of Wellington. This, together with later studies (Chambers et al. 2001; Nielsen et al. 2011), has revealed a similar phylogenetic diversity within the New Zealand geckos to that found among the skinks, although many of these new species remain to be described; only one new species of New Zealand gecko, *Hoplodactylus cryptozoicus*, has been named in the last three decades (Jewell and Leschen 2004).

2.15 A Tribute to Tony (Anthony) Whitaker

Closing this chapter, it would be remiss not to mention the person who has collected the greatest number of new lizard species: Anthony Hume Whitaker (5. ix.1944–2014.ii.20). Whitaker, born in Chesterfield, England, came to New Zealand in 1951 and gained his BSc from the Victoria University of Wellington in 1966 (Bell, 2014). He joined the Animal Ecology Division of the Department of Scientific and Industrial Research (DSIR) and later operated as a private ecological consultant. He was heavily involved in studies of the ecology and distribution of the New Zealand (and later the New Caledonian) herpetofauna. Later, he curated the herpetological collection at the Museum of New Zealand Te Papa Tongarewa. While he only personally described one of his New Zealand lizard discoveries, *Mokopirirakau kahutarae* (Whitaker 1984), he was also instrumental in the discovery of many others, collecting the neotype of *Tiliqua ornata*, the holotypes and at least some of the paratypes of *Leiolopisma pachysomaticum*, *Leiolopisma chloronoton*, *Cyclodina whitakeri*, *Oligosoma longipes*, *Oligosoma stenotis* and *O. townsi* and paratypes of *Leiolopisma nigriplantare maccanni*, *O. hardyi* and *O. toka*. Tony's passion for the New Zealand lizard fauna was also manifested by his compilation, with Bruce Thomas of DSIR, of a detailed bibliography of New Zealand lizards (Whitaker and Thomas 1989) that greatly assisted in the preparation of this review. I gratefully dedicate this chapter to his memory.

Acknowledgements I thank the library staff of the University of Sydney, State Library of New South Wales, and Australian Museum for locating many obscure references and Carrie Browne, Rod Hitchmough and Nicole Schumann for reading and editing a previous draft of this chapter. Images of some of the collectors and describers of New Zealand lizards were supplied by courtesy of Connie Rinaldo and Dana Fisher (Ernst Mayr Library, Museum of Comparative Zoology), Jenni Chrisstoffels (Alexander Turnbull Library), Jean-Claude Stahl (Museum of New Zealand Te Papa Tongarewa), Lucy Spencer (Victorian Parliamentary Library), Margaret Low (Visual Media Library, GNS Science) and Robynne Hayward (State Library of New South Wales).

References

Adams W (1867) [untitled advertisement]. Lyttelton Times 27(2001):3 (20 May 1867)

Adler K (1989) Herpetologists of the past. In: Adler K (ed) Contributions to the history of herpetology, vol 1. Society for the Study of Amphibians and Reptiles, Oxford, pp 5–163

Adler K (2007) Herpetologists of the past. Part 2. In: Adler K (ed) Contributions to the history of herpetology, vol 2. Society for the Study of Amphibians and Reptiles, St Louis, pp 7–273

Adler K (2012) Herpetologists of the past. Part 3. In: Adler K (ed) Contributions to the history of herpetology, vol 3. Society for the Study of Amphibians and Reptiles, Vancouver, pp 9–386

Adler K (2014) Herpetologists of the past. Part 1. In: Adler K (ed) Contributions to the history of herpetology, vol 1, revised and expanded. Society for the Study of Amphibians and Reptiles, Oxford, pp 5–172 + pl 1–96

Anderson W (1967) A journal of a voyage made in His Majesty's Sloop Resolution May 16th 1776. In: Beaglehole JC (ed) The journals of Captain James Cook on his voyages of discovery. III. The voyage of the Resolution and Discovery 1776–1780, Part 2. Cambridge University Press for Hakluyt Society, Cambridge, pp 723–986

Andrews JRH (1986) The southern ark: zoological discovery in New Zealand 1769–1900. Century Hutchinson, Auckland

Andrews JRH (1993) The French and zoological discovery in New Zealand. Tuatara 32:70–74

Angas GF (1847) Savage life and scenes in Australia and New Zealand: being an artist's impressions of countries and people at the antipodes, vol 2. Smith, Elder & Co, London

Anonymous (1825) Nécrologie. Rev Encycl 26:274

Anonymous (1835) Bulletin. Analyse critique. Nouv Ann Voy Sci Géogr (3)6:375–381

Anonymous (1857) Donations to the Australian Museum during April, 1857. Sydney Morn Herald 38(5901):5 (5 May 1857)

Anonymous (1862) The Australian Museum. Sydney Mail 2(102):3 (14 June 1862)

Anonymous (1865a) Port of Auckland. N Z Herald 2(398):4 (21 February 1865)

Anonymous (1865b) The Christy's Minstrels. Colonist 8(830):2 (13 October 1865)

Anonymous (1866) Shipping intelligence. Daily Southern Cross 22(2734):3 (28 April 1866)

Anonymous (1874) Nelson Association for the Promotion of Science and Industry. Trans Proc N Z Inst 6:448–449

Anonymous (1881a) Shipping telegrams. Press 35(4919):2 (24 May 1881)

Anonymous (1881b) [untitled]. N Z Herald 18(6103):4 (9 June 1881)

Anonymous (1881c) Port of Lyttelton. Press 35(4939):2 (16 June 1881)

Anonymous (1899a) Death of an old settler. Colonist 93(9637):2 (16 December 1899)

Anonymous (1899b) Philosophical Institute of Canterbury. Trans Proc New Zealand Inst 31:730–735

Anonymous (1901) Philosophical Institute of Canterbury. Trans Proc N Z Inst 33:569–572

Anonymous (1906) The cyclopedia of New Zealand, vol 5. Nelson, Marlborough, and Westland Provincial districts. Cyclopedia Company, Christchurch

Anonymous (1927) Nelson news. Evening Post 108(29):5 (4 February 1927)

Austen R, Crowley JW (1991) Genteel pagan: the double life of Charles Warren Stoddard. University of Massachusetts, Amherst

Bagnall AG, Peterson GC (1948) William Colenso – Printer, missionary, botanist, explorer, politician, his life and journeys. AH & AW Reed, Wellington

Barrow T (1969) Maori wood sculpture of New Zealand. AH & AW Reed, Wellington

Barwick RE (1955) Studies on the scincid lizard, *Leiolopisma zelandica* (Gray, 1843) with notes on *Leiolopisma aeneum* (Girard, 1857). MSc dissertation. Victoria University of Wellington

Barwick RE (1959) The life history of the common New Zealand skink *Leiolopisma zelandica* (Gray, 1843). Trans R Soc N Z 86(3/4):331–380

Bathgate A (1922) Some changes in the flora and fauna of Otago in the last sixty years. N Z J Sci Technol 4(6):273–283

Bauer AM (1987) The proper Latin designation of Duvaucel's gecko, with comments on specimens of historical note. N Z J Zool 14(4):593–595

Bauer AM, Henle K (1994) Familia Gekkonidae (Reptilia, Sauria). Part I Australia and Oceania. Das Tierreich 109:i–xiii,1–306

Bauer AM, Russell AP (1986) *Hoplodactylus delcourti* n.sp. (Reptilia: Gekkonidae), the largest known gecko. N Z J Zool 13(1):141–148

Bauer AM, Russell AP (1987) *Hoplodactylus delcourti* (Reptilia: Gekkonidae) and the kawekaweau of Maori folklore. J Ethnobiol 7(1):83–91

Bauer AM, Russell AP (1988) Osteological evidence for the prior occurrence of a giant gecko in Otago, New Zealand. Cryptozoology 7:22–37

Bauer AM, Russell AP (1990) Recent advances in the search for the living giant gecko of New Zealand. Cryptozoology 9:66–73

Bayly W (1914) Extract from the journal kept by William Bayly, astronomer, on H.M.S. Adventure, Captain Furneaux, during Capt. Cook's second voyage. In: McNab R (ed) Historical records of New Zealand, vol 2. Government Printer, Wellington, pp 201–218

Beasley AW (2001) The other brother – a brief account of the life and times of Frederick John Knox LRCSEd. J Roy Coll Surg Edinburgh 46:119–123

Beattie H (1920) Nature-lore of the southern Maori. Trans Proc N Z Inst 52:53–77

Bell BD (2014) Anthony Hume Whitaker, MNZM (1944-2014). J Roy Soc N Z 44(2–3):57–60

Bell GE (1976) Ernest Dieffenbach. Rebel and humanist. Dunmore Press, Palmerston North

Bell T (1843) Reptiles. In: Darwin C (ed) The zoology of the voyage of H.M.S. Beagle, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836. Smith Elder & Co, London, p i–vi + 1–51 + pl 1–20

Bell TP, Patterson GB (2008) A rare alpine skink *Oligosoma pikitanga* n. sp. (Reptilia: Scincidae) from Llawrenny Peaks, Fiordland, New Zealand. Zootaxa 1882:57–68

Best E (1909) Maori forest lore: being some account of native forest lore and woodcraft, as also of many myths, rites, customs, and superstitions connected with the flora and fauna of the Tuhoe or Ure-wera district. Part II. Trans Proc N Z Inst 41:231–285

Best S (1988) Here be dragons. J Polynesian Soc 97(3):239–259

Beu AG (1996) Suter, Henry 1841-1918. In: Orange C (ed) Dictionary of New Zealand biography, vol 3. Auckland University Press, Auckland, for Department of Internal Affairs, Wellington, p 494

Beu A, Marshall B, Ponder W (2003) Richard Kenneth ('Dick') Dell, 1920–2002: obituary, bibliography and a list of his taxa. Mollusc Res 23(1):85–99

Bieler R, Petit RE (2012) Molluscan taxa in the publications of the Museum Godeffroy of Hamburg, with a discussion of the Godeffroy sales catalogs (1864–1884), the Journal des Museum Godeffroy (1873-1910), and a history of the museum. Zootaxa 3511:1–80

Biggs B (1981) The complete English–Maori dictionary. Auckland University Press, Auckland

Boulenger GA (1885) Catalogue of the lizards in the British Museum (Natural History), vol I. Geckonidae, Eublepharidae, Uroplatidae, Pygopodidae, Agamidae. Trustees of the British Museum, London

Boulenger GA (1887) Catalogue of the lizards in the British Museum (Natural History), vol III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae. Trustees of the British Museum, London

Boulenger, GA (1902) Description of a new lizard from Pitt Island, near Chatham Island, New Zealand. Ann Mag Nat Hist (7)9(51):196–197

Boulenger GA (1906) Descriptions of two new lizards from New Zealand. Ann Mag Nat Hist (7) 17(100):369–371+pl.x

Boumphrey RS (1964) Alexander Smith's account of the discovery of East Antarctica, 1841. Geogr J 130(1):113–115

Bour R (2012) The Erpétologie Générale (1834–1854) and its authors, Constant Duméril (1774–1860), Gabriel Bibron (1805–1848), and Auguste Duméril (1812–1870). In: Duméril AMC, Bibron G, Duméril AHA (eds) Erpétologie générale ou histoire naturelle complète des reptiles, vol 1, facsimile edn. Society for the Study of Amphibians and Reptiles, Ithaca, pp 5–107

Boyd MMM (1934) Notes on the structure and life history of *Hoplodactylus maculatus* (Gray). MSc dissertation. Victoria University of Wellington

Boyd MMM (1935) Further notes on the development of *Hoplodactylus maculatus*. MSc dissertation. Victoria University of Wellington

Boyd MMM (1939) 1. The structure of the ovary and the formation of the corpus luteum in *Hoplodactylus maculatus*, Gray. II: The foetal membranes and placentation in *Hoplodactylus maculatus*, Gray. PhD dissertation, University of London

Boyd MMM (1940) The structure of the ovary and the formation of the corpus luteum in *Hoplodactylus maculatus*, Gray. Q J Microsc Sci 82(2):337–376+pl.13–19

Boyd MMM (1942) The oviduct, foetal membranes and placentation in *Hoplodactylus maculatus* Gray. Proc Zool Soc Lond Ser A 112(1–2):65–104+pl.I

Branagan DF (1983) Samuel Stuchbury and his manuscripts. In: Hoare ME, Bell LG (eds) In search of New Zealand's scientific heritage. R Soc N Z Bull 21:7–15

Branagan DF (1993) Samuel Stutchbury: a natural history voyage to the Pacific, 1825–27 and its consequences. Arch Nat Hist 20(1):69–91

Branagan DF, Vallance TG (1976) Stutchbury, Samuel (1798–1859). In: Searle G, Ward R (eds) Australian dictionary of biography, vol 6. Melbourne University Press, Melbourne, pp 216–217

Brownlie M (1993) Balfour, David Paton 1841–1894. In: Orange C (ed) Dictionary of New Zealand biography, vol 2. Bridget William Books for Department of Internal Affairs, Wellington, p 22

Brown-May A, May TW (1997) 'A mingled yarn': Henry Edwards, thespian and naturalist, in the Austral land of plenty. Hist Rec Aust Sci 11(3):407–418

Buchanan JG (1956) The gross and minute anatomy of the heart of the lizard, *Leiolopisma grande* (Gray). Trans R Soc N Z 84(1):103–120

Buick TL (1928) The French at Akaroa. An adventure in colonization. New Zealand Book Depot, Wellington

Buller, WL (1871) A list of the lizards inhabiting New Zealand, with descriptions. Trans Proc N Z Inst 3(Trans):4–11, 56+pl.2

Buller WL (1873) [Untitled]. Trans Proc N Z Inst 5:404–405

Buller WA [in error, WL] (1877) Description of a new lizard, *Naultinus pulcherrimus*. Trans Proc N Z Inst 9:326–327+pl.17

Buller WL (1881) Description of a new species of lizard of the genus *Naultinus*. Trans Proc N Z Inst 13:419–420

Buller WL (1896) [Untitled]. Trans Proc N Z Inst 28:735

Burns P (ed H Richardson) (1989) Fatal success: a history of the New Zealand Company. Heinemann Reed, Auckland

Byrne TB (2007) The Pandora survey: the completion of the 1848-1856 Great Survey of New Zealand by HMS Pandora, together with an account of its genesis and initial phase. Author, Auckland

Cadbury D (2000) Terrible lizard. The first dinosaur hunters and the birth of a new science. Henry Holt & Co, New York

Calaby JH (1967) MacGillivray, John (1821–1867). In: Shaw AGL, Clark CMH (eds) Australian dictionary of biography, vol 2. Melbourne University Press, Carlton, pp 167–168

Chambers GK, Boon WM, Buckley TR, Hitchmough RA (2001) Using molecular methods to understand the Gondwanan affinities of the New Zealand biota: three case studies. Aust J Bot 49(3):377–387

Chapple DG, Patterson GB (2007) A new skink species (*Oligosoma taumakae* sp. nov.; Reptilia: Scincidae) from the Open Bay Islands, New Zealand. N Z J Zool 34(4):347–357

Chapple DG, Patterson GB, Bell T, Daugherty CH (2008a) Taxonomic revision of the New Zealand Copper Skink (*Cyclodina aenea*: Squamata: Scincidae) species complex, with descriptions of two new species. J Herpetol 42(3):437–452

Chapple DG, Patterson GB, Gleeson DM, Daugherty CH, Ritchie PA (2008b) Taxonomic revision of the marbled skink (*Cyclodina oliveri*, Reptilia: Scincidae) species complex, with a description of a new species. N Z J Zool 35(2):129–146

Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). Mol Phylogenet Evol 52(2):470–487

Chapple DG, Bell TP, Chapple SNJ, Miller KA, Daugherty CH, Patterson GB (2011) Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma inconspicuum*; Reptilia: Scincidae) species complex. Zootaxa 2782:1–33

Cheeseman, TF (1907) Notes on certain Maori carved burial-chests in the Auckland Museum. Trans Proc N Z Inst 39:451–456 + pl. xii-xiii

Colenso W (1878) Contributions towards a better knowledge of the Maori race. Trans Proc N Z Inst 11:77–106

Colenso W (1880) Notes and observations on the animal economy and habits of one of our New Zealand lizards, supposed to be a new species of *Naultinus*. Trans Proc N Z Inst 12:251–264

Colenso W (1885) Description of a small lizard, a species of *Naultinus*, supposed to be new to science. Trans Proc N Z Inst 17:149–151

Colenso W (1887) Further notes and observations on the gestation, birth and young of a lizard, a species of *Naultinus*. Trans Proc N Z Inst 19:147–150

Cook J (1784) A voyage to the Pacific Ocean undertaken by the command of his Majesty for making discoveries in the Northern Hemisphere performed under the direction of Captains, Cook, Clerke and Gore in His Majesty's ships the Resolution and Discovery; in the years 1776, 1777, 1778, 1779, and 1780, vol 1. W & A Strahan, London

Cooper GA (1851) Journal of an expedition overland from Auckland to Taranaki, by way of Rotorua, Taupo, and the West Coast. Undertaken in the summer of 1849–50, by his Excellency the Governor-in-chief of New Zealand. Williamson & Wilson, Auckland

Cooper RC (1970) John Edgerley, botanist, in New Zealand. Rec Auckland Inst Mus 7:123–136

Cope ED (1869) Observations on reptiles of the Old World. Art. II. Proc Acad Nat Sci Phila 20:316–323

Crane MD (1983) Samuel Stutchbury (1798–1859), naturalist and geologist. Notes Rec R Soc Lond 37(2):189–200

Crawford JC (1880) Recollections of travel in New Zealand and Australia. Trubner & Co, London

C[uvier] F (1824) Notice sur les voyages de M. Duvaucel. Rev Encycl 21:257–267

Cuvier G (1821) Notice sur les voyages de MM. Diard et Duvaucel, naturalistes français, dans les Indes orientales et dans les îles de la Sonde. Rev Encycl 10:473–482

Daugherty CH, Patterson GB, Thorn CJ, French DC (1990) Differentiation of the members of the New Zealand *Leiolopisma nigriplantare* species complex (Lacertilia: Scincidae). Herpetol Monogr 4:61–76

David A (1995) The voyage of HMS Herald to Australia and the South-west Pacific 1852–1861 under the command of Captain Henry Mangles Denham. Miegunyah Press (Melbourne University Press), Carlton

Dawson GE, Dawson EW (1958) Birds of the Cook Strait Islands, collected by Professor Hugo Schauinsland in 1896 and 1897. Notornis 8(2):39–42, 47–49

de Hamel FA, McInnes HM (1971) Lizards as vectors of human salmonellosis. J Hygiene 69 (2):247–253

Dell RK (1990) Hector, James 1834–1907. In: Oliver WH (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin for Department of Internal Affairs, Wellington, pp 183–184

Dell RK (1998a) Oliver, Walter Reginald Brook 1883-1957. In: Orange C (ed) Dictionary of New Zealand biography, vol 4. Auckland University Press, Auckland, for Department of Internal Affairs, Wellington, pp 389–390

Dell RK (1998b) Falla, Robert Alexander 1901–1979. In: Orange C (ed) Dictionary of New Zealand biography, vol 4. Auckland University Press, Auckland, for Department of Internal Affairs, Wellington, pp 166–167

D'Estrey M (1892) Étude ethnographique sur le lézard chez les peuples Malais et Polynésiens. L'Anthropologie 3(6):711–719

Dieffenbach E (1843) Travels in New Zealand; with contributions to the geography, geology, botany, and natural history of that country, 2 vols. John Murray, London

Doré AB (1919) The occurrence of haemogregarina in New Zealand lizards. N Z J Sci Technol 2 (3):163–164

Downes TW (1937) Maori mentality regarding the lizard and Taniwha in the Whanganui River area. J Polynesian Soc 46(4):206–224

Dumbleton LJ (1947) Trombidiidae (Acarina) from the Solomon Islands and New Zealand. Trans R Soc N Z 76(3):409–413

Duméril AMC, Bibron G (1836) Erpétologie générale ou histoire naturelle complete des reptiles, vol 3. Librairie Encyclopédique de Roret, Paris

Duméril AMC, Bibron G (1839) Erpétologie générale ou histoire naturelle complete des reptiles, vol 5. Librairie Encyclopédique de Roret, Paris

Duméril AMC, Duméril A (1851) Catalogue méthodique de la collection des reptiles. Gide et Baudry, Paris

Duméril AMC, Bibron G, Duméril A (1854) Erpétologie générale ou histoire naturelle complete des reptiles, Atlas. Librairie Encyclopédique de Roret, Paris

Dumont d'Urville J (1830) Voyage de la corvette l'Astrolabe execute par ordre du Roi, pendant les années 1826–1827–1828–1829. Histoire du Voyage, vol 2. J. Tastu, Paris

Dumont d'Urville J (1846) Voyage au Pole Sud et dans l'Oceanie sur les corvettes l'Astrolabe et La Zélée, execute par ordre du Roi pendant les années 1837–1838–1839–1840. Histoire du Voyage, vol 9. Gide et Cie, Paris

Dunmore J (1981) The expedition of the St Jean-Baptiste to the Pacific 1769–1770, from the journals of Jean de Surville and Guillaume Labé. Hakluyt Society (Series 2, No. 158), London

Dunmore J (1990) Surville, Jean François Marie de 1717–1770. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 411–412

Endersby J (2008) Imperial nature. Joseph Hooker and the practices of Victorian science. University of Chicago Press, Chicago

Fardy BD (1985) William Epps Cormack. Newfoundland pioneer. Creative Publishers, St. John's

Fawcett JD (1964a) The life history and ecology of *Sphenomorphus pseudornatus* (McCann). Bull Zool Dept, Univ Auckland 1:25–26

Fawcett JD (1964b) The life history and ecology of *Sphenomorphus pseudornatus* McCann (Lacertilia, Scincidae). MSc dissertation, University of Auckland

Fawcett JD (1970) Reproduction in the New Zealand skink, *Sphenomorphus pseudornatus*. J Colorado-Wyoming Acad Sci 7(1):43

Fischer JG (1882) Herpetologische bemerkungen vorzugsweise über Stücke der Sammlung des Naturhistorischen Museum in Bremen. Abh Naturwiss Ver Bremen 7(3):225–238+pl.XIV–XVII

Fitzinger L (1843) Systema reptilium fasciculus primus, amblyglossae. Braumüller et Seidel, Vindobonae

Fitzinger LJ (1860) Die Ausbeute der österreichischen Naturforscher an Säugethieren und Reptilien während der Weltumsegelung Sr. Majestät Fregatte Novara. Sitzungsber Kaiserl Akad Wiss, Wien, Math-Naturwiss Classe 42(24):383–416

Fleming CA (1990) Hochstetter, Christian Gottlieb Ferdinand von 1829–1884. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 199–200

Fomison A (2013) Maori rock art in North Otago and South Canterbury. A guide to the interpretation of its styles and subject matter. Rec Canterbury Mus 27:52–95

Frauenfeld G (1860) Notizen, gesammelt während meines Aufenthaltes auf Neu-holland, Neuseeland und Taiti, bei der Fahrt Sr. Majestät Fregatte Novara in jenen Gewässern. Sitzungsber Kaiserl Akad Wiss, Wien, Math-Naturwiss Classe 38(27):717–748

Freeman AND, Tunnicliff GA (1997) Recent vertebrate types in the Canterbury Museum, Christchurch, New Zealand. Rec Canterbury Mus 11:1–16

Fulton R (1904) The Kokoperoa or Koekoea, Long-tailed Cuckoo (*Urodynamis taitensis*): an account of its habits, description of a nest containing its (supposed) egg, and a suggestion as to how the parasitic habit in birds has become established. Trans Proc N Z Inst 36:113–148

Galbreath R (1990) Buller, Walter Lawry 1838–1906. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 53–54

Garman S (1901) Some reptiles and batrachians from Australasia. Bull Mus Comp Zool Harvard Coll 39(1):1–14+pl.1–2

Gibbons JRH, Clunie F (1984) Brief notes on the voracious gecko, *Gehyra vorax*. Domodomo 2 (1):34–36

Gill BJ (1975) Aspects of the ecology, morphology and taxonomy of two skinks (Reptilia: Lacertilia) in the coastal Manawatu. BSc(Hons) dissertation, Massey University

Gill BJ (1976) Aspects of the ecology, morphology and taxonomy of two skinks (Reptilia: Lacertilia) in the coastal Manawatu area of New Zealand. N Z J Zool 3(2):141–157

Gill BJ (1983) Type specimens of amphibians, reptiles, birds and mammals in the Auckland Institute and Museum. Rec Auckland Inst Mus 20:203–215

Gill BJ (1985) Subfossil bones of a large skink (Reptilia; Lacertilia) from Motutapu Island, New Zealand. Rec Auckland Inst Mus 22:69–76

Gill BJ (2014) Evan Graham Turbott, M.Sc., Q.S.O. 1914–2014. Notornis 62(1):51–56

Gill BJ, Froggatt JMA (2014) The Indian herpetological collections of Charles McCann. Rec Auckland Mus 49:29–37

Gill BJ, Whitaker AH (1996) New Zealand frogs and reptiles. David Bateman, Auckland

Girard C (1857) Descriptions of some new reptiles, collected by the United States Exploring Expedition, under the command of Capt. Charles Wilkes, U.S.N. Fourth part. – Including the species of saurians, exotic to North America. Proc Acad Nat Sci Phila 9:195–199

Girard C (1858) Herpetology. In: United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N., vol 20. JB Lippincott, Philadelphia, p i–xvii + 1–496

Godley EJ (1998) Biographical notes (31): Arthur Dendy, D.Sc. (Manchester); Hon. Mem. N.Z. Inst.; FLS; F.R.S. (1865–1925). N Z Bot Soc Newslett 53:25–27

Godley EJ (2004) Biographical notes (54): John Carl Ernest Dieffenbach (1811–1855). N Z Bot Soc Newslett 76:31–35

Godley EJ (2007) Biographical notes (66): Joseph Robert Annabell (1857–1924). N Z Bot Soc Newslett 88:14–17

Goode GB (1891) The published writings of Dr. Charles Girard. Bull United States Natl Mus 41:i–vi, 1–141

Gray JE (1834) Characters of two new genera of reptiles (*Geoemyda* and *Gehyra*). Proc Zool Soc Lond 2:99–101

Gray JE (1842a) Description of some new species of reptiles, chiefly from the British Museum collection. In: Gray JE (ed) The zoological miscellany. Truettel, Wurtz & Co, GB Sowerby, W Wood, London, pp 57–59

Gray JE (1842b) Descriptions of two hitherto unrecognised species of reptiles from New Zealand; presented to the British Museum by Dr. Dieffenbach. In: Gray JE (ed) The zoological miscellany. Truettel, Wurtz & Co, GB Sowerby, W Wood, London, p 72

Gray JE (1843) Descriptions of the Reptiles and Amphibia hitherto observed in New Zealand. In: Dieffenbach, E Travels in New Zealand; with contributions to the geography, geology, botany, and natural history of that country, vol 2. John Murray, London, pp 202–206

Gray JE (1845a) Reptiles. In: Richardson J, Gray JE (eds) Zoology of the voyage of H.M.S. Erebus & Terror, under the command of Captain Sir James Clark Ross, R.N., F.R.S., during the years 1839 to 1843, vol 2. Longman, Brown, Green & Longmans, London, p 1–8 + pl 1–4, 8–9, 12–14, 20

Gray JE (1845a) Catalogue of the specimens of lizards in the collection of the British Museum. Edward Newman, London

Gray JE (1867) The lizards of Australia and New Zealand in the collection of the British Museum (with 18 plates of the new species, by Mr. Ford). Bernard Quaritch, London

Gray, JE (1869) *Naultinus lineatus*, a new lizard from New Zealand. Ann Mag Nat Hist (4)3 (15):243

Guibé J (1954) Catalogue des types de lézards du Muséum National d'Histoire Naturelle. Colas, Paris

Gunther AE (1975) A century of zoology at the British Museum though the lives of two keepers 1815–1914. Wm Dawson, London

Hamilton A (1898) On rock pictographs in South Canterbury. Trans Proc N Z Inst 30:24–29+pl I–X

Hamilton A (1903) Notes on a bone pendant in the form of a lizard(?), found on the sandhills at Wainui; and on some other bone objects. Trans Proc N Z Inst 35:111–113+pl viii–ix

Hardy GS (1976) Taxonomic and zoogeographic studies of the New Zealand Scincidae. PhD dissertation, Victoria University of Wellington

Hardy GS (1977) The New Zealand Scincidae (Reptilia: Lacertilia): a taxonomic and zoogeographic study. N Z J Zool 4(3):221–325

Hardy GS (1979) The karyotypes of two scincid lizards, and their bearing on relationships in genus *Leiolopisma* and its relatives (Scincidae: Lygosominae). N Z J Zool 6(4):609–612

Hardy GS (1982) Review of some aspects of New Zealand skink taxonomy. In: Newman DG (ed) New Zealand herpetology. Proceedings of a symposium held at the Victoria University of Wellington 29-31 January 1980. New Zealand Wildlife Service Occasional Publication 2, pp 349–357

Hardy GS, Hicks GRF (1980) Proposed removal of *Leiolopisma* (?) *fasciolare* from the checklist of New Zealand Scincidae (Reptilia: Lacertilia), and a note on the name *Hombronia*. N Z J Zool 7(3):425–426

Hector J, Tregear E (1899) Untitled discussion on the “kumi”. Trans Proc N Z Inst 31:717–718

Hiroa Te R [Buck P] (1949) The coming of the Maori, 2nd edn. Whitcoulls, Christchurch

Hitchmough RA (1997) A systematic revision of the New Zealand Gekkonidae. PhD dissertation, Victoria University of Wellington

Hitchmough RA, Patterson GB (2010) *Cyclodina aenea* Girard, 1857 (currently *Oligosoma aeneum*; Reptilia, Squamata, Scincidae): proposed conservation of the specific name and suppression of the senior subjective synonym *Tiliqua ornata* Gray, 1843 (currently *Oligosoma ornatum* Gray, 1843). Bull Zool Nomencl 67(4):307–313

Hitchmough RA, Patterson GB (2011) Comment on the proposed conservation of the specific name of *Cyclodina aenea* Girard, 1857 (currently *Oligosoma aeneum*; Reptilia, Squamata, Scincidae) and suppression of the senior subjective synonym *Tiliqua ornata* Gray, 1843 (currently *Oligosoma ornatum*). Bull Zool Nomencl 68(2):144

Hitchmough RA, Patterson GB, Chapple DG (2016) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Holder LA (1960) The comparative morphology of the axial skeleton in the Australian Gekkonidae. J Linn Soc (Zool) 44(297):300–335

Hooker JD (1895) David Lyall M.D. J Bot Br Foreign 33:209–211

Hordern M (1989) Mariners are warned! John Lort Stokes and H.M.S. Beagle in Australia 1837–1843. Miegunyah Press (Melbourne University Press), Carlton

Howes HS (2011) ‘It is not so!’ Otto Finsch, expectations and encounters in the Pacific, 1865–85. Hist Rec Aust Sci 22(1):32–52

Howse D (2004) Bayly, William (bap. 1738, d. 1810). In: Matthew HCG, Harrison B (eds) Oxford dictionary of national biography, vol 4. Oxford University Press, Oxford, p 468

Hutton FW (1872) Notes on the lizards of New Zealand, with descriptions of two new species. Trans Proc N Z Inst 4:167–172

Hutton FW (1873) On the geographic relations of the New Zealand fauna. Trans Proc N Z Inst 5:227–256

Hutton FW (1904) Index faunae Novae Zelandiae. Dulau, London

Hutton FW, Drummond J (1904) The animals of New Zealand. An account of the colony’s air-breathing vertebrates. Whitcombe & Tombs, Christchurch

Jewell TR, Leschen RAB (2004) A new species of *Hoplodactylus* (Reptilia: Pygopodidae) from the Takitimu Mountains, South Island, New Zealand. Zootaxa 792:1–11

Kaufman MH (2001) Frederick Knox, younger brother and assistant of Dr Robert Knox: his contribution to “Knox’s Catalogues”. J Roy Coll Surg Edinburgh 46:44–56

Keevil JJ (1933) William Anderson, 1748-1778 master surgeon, Royal Navy. Ann Med Hist (ns)5 (6):511–524

King M (1981) The collector. A biography of Andreas Reischek. Hodder & Stoughton, Auckland

Kirk T (1896) The displacement of species in New Zealand. Trans Proc N Z Inst 28:1–27

K[line] B (1912) Agassiz’s right-hand man. Boston Evening Transcript 83(133):20 (5 Jun 1912)

Kloosterman AMJ (1976) Discoverers of the Cook Islands and the names they gave. Cook Islands Library and Museum, Rarotonga

Knox FJ (1870) On the anatomy of the *Naultinus greyii*, Gray, or brown tree lizard of New Zealand. Trans Proc N Z Inst 2:20–21

Knox FJ (1873) Observations on *Naultinus pacificus*, Gray. Trans Proc N Z Inst 5:307–308

Laird M (1949) Studies on the haematozoa of New Zealand and some adjacent islands. MSc dissertation, Victoria University of Wellington

Laird M (1951) *Plasmodium lygosomae* n. sp., a parasite of a New Zealand skink, *Lygosoma moco* (Gray, 1839). J Parasitol 37(2):183–189

Lescure J (2015) René-Primevère Lesson (1794–1849), pharmacien de la Marine, voyageur-naturaliste et herpétologiste. Bull Soc Herpetol Fr 155:1–50

Lesson R-P (1828) Observations générales sur les reptiles observés dans le voyage autour du monde de la corvette La Coquille. Ann Sci Nat 13:369–394

Lesson R-P (1830) Observations generals sur les reptiles recueillis dans le voyage dl la corvette La Coquille. In: Duperrey LI (ed) Voyage autour du monde execute par ordre du Roi, sur la corvette de Sa Majeste, La Coquille, pendant les années 1822, 1823, 1824 et 1825, vol 2, Zoologie, tome. Arthus Bertrand, Paris, pp 1–23

Lesson [R-]P (1839) Voyage autour du monde entrepris par ordre du gouvernment sur la corvette la Coquille, vol 2. P. Pourrat Fréres, Paris

Lewis D (1982) The Maori. Heirs of Tane. Orbis, London

Lucas AHS, Frost C (1897) The lizards (Lacertilia) indigenous to New Zealand. Trans Proc N Z Inst 29:264–280

Mackay D (1990) Colenso, William 1811–1899. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 87–89

Matthews REF (1988) Charles Alexander Fleming. 9 September 1916–11 September 1987. Biogr Mem Fellows R Soc 34:178–203

McCallum J (1980) The locality of Flat Island. Herpetofauna 11(2):5–6

McCallum J (1986) Evidence of predation by kiore upon lizards from the Mokohinau Islands. N Z J Ecol 9:83–87

McCann C (1955) The lizards of New Zealand. Gekkonidae and Scincidae. Dominion Mus Bull 17:1–127

McLachlan H (1935) Records of a family 1800–1933. Pioneers in education, social service and liberal religion. Manchester University Press, Manchester

McLean D (1990) Dieffenbach, Johann Karl Ernst 1811–1855. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 107–108

McLintock AH (1966) Second New Zealand Company. In: An encyclopaedia of New Zealand, vol 2. RE Owen, Government Printer, Wellington, pp 658–660

Miskelly CM (2012) Bird names commemorating Edward Stead. Notornis 59(1–2):7–14

Molloy BPJ (1990) Sinclair, Andrew 1794–1861. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, p 397

Morton J (1998) McGregor, William Roy 1894–1977. In: Orange C (ed) Dictionary of New Zealand biography, vol 4. Auckland University Press, Auckland, for Department of Internal Affairs, Wellington, p 310

Murray JE (1990) Stack, James West 1835-1919. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 403–404

Nathan S (ed) (2015) James Hector: explorer, scientist, leader. Miscellaneous Publication 140. Geoscience Society of New Zealand, Lower Hutt

Natusch S (1978) The cruise of the Acheron. Her Majesty's steam vessel on survey in New Zealand waters 1848–51. Whitcoulls, Christchurch

Newman DG (ed) (1982) New Zealand herpetology. In: Proceedings of a symposium held at the Victoria University of Wellington 29–31 January 1980. New Zealand Wildlife Service Occasional Publication 2

Nielsen SV, Bauer AM, Jackman TR, Hitchmough R, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol 59:1–22

Panning A (1956) Beiträge zur Geschichte des Zoologischen Staatsinstituts und Zoologischen Museums in Hamburg. 2 Teil. Mitt Hamburgischen Zool Mus Inst 54:1–20

Parkinson P (1983) William Swainson 1789-1855: relics in the Antipodes. In: Hoare ME, Bell LG (eds) In search of New Zealand's scientific heritage. R Soc N Z Bull 21:49–63

Parton HN (1993) Hutton, Frederick Wollaston 1836–1905. In: Orange C (ed) Dictionary of New Zealand biography, vol 2. Bridget William Books for Department of Internal Affairs, Wellington, pp 238–239

Patterson GB (1985a) The ecology and taxonomy of the common skink *Leiolopisma nigriplantare maccanni* in tussock grasslands in Otago. PhD dissertation, University of Otago

Patterson GB (1985a) A taxonomic reconsideration of the common skink, *Leiolopisma nigriplantare maccanni*, in Otago tussock grassland. N Z J Ecol 8:151–152

Patterson GB (1997) South Island skinks of the genus *Oligosoma*: description of *Oligosoma longipes* n. sp. with redescription of *O. otagense* (McCann) and *O. waimatense* (McCann). J R Soc N Z 27(4):439–450

Patterson GB, Bell TP (2009) The Barrier skink *Oligosoma judgei* n. sp. (Reptilia: Scincidae) from the Darran and Takitimu Mountains, South Island, New Zealand. Zootaxa 2271:43–56

Patterson GB, Daugherty CH (1990) Four new species and one new subspecies of skinks, genus *Leiolopisma* (Reptilia: Lacertilia: Scincidae) from New Zealand. J R Soc N Z 20(1):65–84, 252

Patterson GB, Daugherty CH (1994) *Leiolopisma stenotis*, n. sp., (Reptilia: Lacertilia: Scincidae) from Stewart Island, New Zealand. J R Soc N Z 24(1):125–132

Patterson GB, Daugherty CH (1995) Reinstatement of the genus *Oligosoma* (Reptilia: Lacertilia: Scincidae). J R Soc N Z 25(3):327–331

Patterson GB, Hitchmough RA, Chapple DG (2013) Taxonomic revision of the ornate skink (*Oligosoma ornatum*; Reptilia: Scincidae) species complex from northern New Zealand. Zootaxa 3736(1):54–68

Percival E (1941) *Trichomonas hoplodactyli* n. sp. from a New Zealand gecko. Rec Canterbury Mus 4(7):373–375

Peters W (1867) Herpetologische notizen. Monatsber königl Preussischen Akad Wiss Berlin 1867:13–37

Peters W (1873) Eine mitteilung über neue saurier (*Spoeriodactylus*, *Anolis*, *Phrynosoma*, *Tropidolepisma*, *Lygosoma*, *Ophioscincus*) aus Centralamerika, Mexico und Australien. Monatsber königl Preussischen Akad Wiss Berlin 6:738–747

Pickering C (1848) The races of man: and their geographical distribution. In: Wilkes C (ed) United States exploring expedition. During the years 1838, 1839, 1840, 1841, 1842, vol 9. Charles C Little and James Brown, Boston, viii+447p

Porter F (1990) Williams, William 1800–1878. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 597–598

Porter F (1993) Atkinson, Arthur Samuel 1833–1902. In: Orange C (ed) Dictionary of New Zealand biography, vol 2. Bridget William Books for Department of Internal Affairs, Wellington, pp 13–14

Pottier de l'Horne [Horme] J (1914) Extrait du journal de Pottier de l'Horne, Lieutenant du vaisseau le St. Jean Baptiste pour le voyage des découvertes dans le Sud commencé en 1769 et fini en 1773: Description et remarques de la Baie Lauriston a la N'velle Zélande, des habitants, du terrain et des productions de la partie de cette terre que nous avons fréquentée. In: McNab R (ed) Historical records of New Zealand, vol 2. Government Printer, Wellington, pp 314–342

Proust de la Gironière M (2002) La France en Nouvelle-Zélande 1840–1846. Un vaudeville colonial. Éditions du Gerfaut, Paris

Raeside JD (1990) Thierry, Charles Philippe Hippolyte de 1793–1864. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, p 533

Rennie H (1990) Gillies, Thomas Bannatyne 1828–1889. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 149–150

Robb J (1970) A new skink of the genus *Leiolopisma* from New Zealand. Proc Kon Nederlandse Akad Wetensch C 73(2):228–229

Robb J (1975) Two new skinks of the genus *Leiolopisma* from New Zealand. Proc Kon Nederlandse Akad Wetensch C 78(5):477–484

Robb J (1977) A revision of the synonymy of three species of leiolopismid skinks from New Zealand. Bull Br Mus Nat Hist (Zool) 31(6):303–310

Robb J (1980) Three new species of gekkonid lizards, genera *Hoplodactylus* Fitzinger and *Heteropholis* Fischer, from New Zealand. Nat Mus N Z Rec 1(19):305–310

Robb J, Hitchmough RA (1980) Review of the genus *Naultinus* Gray (Reptilia: Gekkonidae). Rec Auckland Inst Mus 16:189–200

Robb J, Rowlands RPV (1977) Reinstatement of *Hoplodactylus maculatus* (Boulenger) with redescription of *H. pacificus* (Gray) (Reptilia: Squamata: Gekkonidae). Rec Auckland Inst Mus 14:133–142

Rorke J (2000) Sladden, Bernard 1879–1961. In: Orange C (ed) Dictionary of New Zealand biography, vol 5. Auckland University Press, Auckland, for Department of Internal Affairs, Wellington, pp 479–480

Sack PG (1972) Finsch, Otto (1839–1917). In: Nairn B, Serle G, Ward R (eds) Australian dictionary of biography, vol 4. Melbourne University Press, Melbourne, pp 170–171

Scheps B (2005) Das verkaufte Museum. Die Südsee-Unternehmungen des Handelshauses Joh. Ces. Godeffroy & Sohn, Hamburg, und die Sammlungen "Museum Godeffroy". Abh Naturwiss Ver Hamburg 40:1–307

Scherzer K (1862) Reise der Österreichischen Fregatte Novara um die Erde, in den Jahren 1857, 1858, 1859, unter den Besehlen des Commodore B. von Wüllerstorf-Urbair. Beschreibender Theil, vol 3. Kaiserlich-Königlichen Hof- und Staatsdruckerei, Wien

Scofield RP, Cooper JH, Turey ST (2012) A naturalist of the very first order: Percy William Earl (1811–1846) in New Zealand. Rec Canterbury Mus 26:1–19

Shand-Tucci D (2003) The crimson letter: Harvard, homosexuality, and the shaping of American culture. St Martins Press, New York

Shea GM (1995) John Edward Gray, Albert Günther, and the lizards of Australia and New Zealand. In: Adler K (ed) The lizards of Australia and New Zealand, facsimile edn. Society for the Study of Amphibians and Reptiles, Ithaca, pp iii–viii

Shea GM (2000) The earliest taxonomic description and illustration of an Australian reptile: another historical first for bluetongue lizards (Squamata: Scincidae: *Tiliqua*). Pap Proc R Soc Tasmania 134:79–82

Shea GM (2004) The Horn expedition (1894) to Central Australia: new directions in Australian herpetology. Bonner Zool Beitr 52(3/4):245–273

Shea GM (2015) From lineages to webs: a history of the Australian Society of Herpetologists. Aust J Zool 62(6):431–447

Shortland E (1856) Traditions and superstitions of the New Zealanders: with illustrations of their manners and customs. Longman, Brown, Green, Longmans & Roberts, London

Simmons ER (1990) Pompallier, Jean Baptiste François 1801–1871. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 349–350

Simpson MJA (1983)The contribution of the French to the botany of Banks Peninsula. In: Hoare ME, Bell LG (eds) In search of New Zealand's scientific heritage. R Soc N Z Bull 21:63–70

Skinner HD (1964) Crocodile and lizard in New Zealand myth and material culture. Rec Otago Mus Anthropol 1:1–43

Smith MA (1933a) Remarks on some Old World geckoes. Rec Indian Mus 35:9–19

Smith MA (1933b) The type locality of the gecko, *Hoplodactylus duvaucelii* Dum. and Bibr. Rec Indian Mus 35:377

Sorrenson MPK (1990) Mantell, Walter Baldock Durrant 1820–1895. In: Oliver WB (ed) Dictionary of New Zealand biography, vol 1. Allen & Unwin, New Zealand for Department of Internal Affairs, Wellington, pp 267–268

Stack JW (1874) On the disappearance of the larger kinds of lizard from North Canterbury. Trans Proc N Z Inst 7:295–297

Stanton W (1975) The Great United States Exploring Expedition of 1838–1842. University of California Press, Berkeley

Staphleu FA, Cowan R (1983) Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types, vol 4, 2nd edn. Bohn, Schultema Holkema, Utrecht

Steindachner F (1867) Reptilien. In: von Wüllerstorf-Urbair B (ed) Reise der Österreichischen Fregatte Novara um die erde in den Jahren 1857, 1858, 1859. Zoologischer Theil. Erster Band (Wirbelthiere). Kaiserlich-Königlichen Hof- und Staatsdrucke, Wien, pp 1–98 + pl I–III

Stephens J (1968) "Brother Fred" and the two cultures: New Zealand's first librarian. N Z Libraries 31(5):175–198

Stephens LD, Calder DR (2006) Seafaring scientist. Alfred Goldsborough Mayor, pioneer in marine biology. University of South Carolina Press, Columbia

Stephenson NG (1939) The occurrence of the genus *Hoplodactylus* in New Zealand and some aspects of the structure of *Hoplodactylus pacificus*. MSc dissertation, University of Auckland

Stephenson NG (1948) A note on the occurrence of the genus *Hoplodactylus* Fitzinger in New Zealand. Rec Auckland Inst Mus 3:339–341

Stephenson NG (1960) The comparative osteology of Australian geckos and its bearing on their morphological status. J Linn Soc (Zool) 44(297):278–299

Stephenson NG, Stephenson EM (1956) The osteology of the New Zealand geckos and its bearing on their morphological status. Trans R Soc N Z 84(2):341–358

Story GM (1976) Cormack, William Eppes (Epps). In: Halpenny FG, Hamelin J (eds) Dictionary of Canadian biography, vol 9. University of Toronto, Toronto, pp 158–162

Stutchbury S (1996) Science in a sea of commerce: the journal of a South Seas trading venture (1825–27). D.F. Branagan, Northbridge

Taylor, R (1848) A leaf from the natural history of New Zealand; or, a vocabulary of its different productions, etc., etc., with their native names. Robert Stokes, Wellington

Taylor R (1870) Maori and English dictionary. George T. Chapman, Auckland

Thomas BW (1981) *Hoplodactylus rakiurae* n. sp. (Reptilia: Gekkonidae) from Stewart Island, New Zealand, and comments on the taxonomic status of *Heteropholis nebulosus* McCann. N Z J Zool 8(1):33–47

Tiedemann F, Häupl M, Grillitsch H (1994) Katalog der Typen der Herpetologischen Sammlung nach dem Stand vom 1. Jänner 1994. Kat wiss Samml Naturhist Mus Wien 10, Vertebrata 4:1–102

Tizard TH, Moseley HN, Buchanan JY, Murray J (1885) Narrative of the cruise of H.M.S. Challenger with a general account of the scientific results of the expedition, vol 1, first part. Her Majesty's Stationary Office, Edinburgh

Towns DR, Hitchmough RA, Perrott J (2016) Conservation of New Zealand lizards: a fauna not forgotten by undervalued? Chap. 11. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Tregear E (1891) The Maori-Polynesian comparative dictionary. Lyon & Blair, Wellington

Tregear E (1904) The Maori race. A D Willis, Wanganui

Turbott EG (1998) Stead, Edgar Fraser 1881–1949. In: Orange C (ed) Dictionary of New Zealand biography, vol 4. Auckland University Press, Auckland, for Department of Internal Affairs, Wellington, pp 491–492

von Hochstetter F (1863) Neu-Seeland. Cotta'scher Verlag, Stuttgart

Werner F (1895) Zwei neue australische *Lygosoma*-Arten. Verh k-k Zool-bot Ges Wien 45 (1):21–22

Werner F (1901) Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896–8197). Zool Jahrb Abt Syst, Geog Biol Thiere 14(5):380–387

Wheeler A (1997) Zoological collections in the early British Museum: the Zoological Society's museum. Arch Nat Hist 24(1):89–126

Whitaker AH (1973) Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). Proc N Z Ecol Soc 20:121–130

Whitaker AH (1984) *Hoplodactylus kahutarae* n.sp. (Reptilia: Gekkonidae) from the Seaward Kaikaoura Range, Marlborough, New Zealand. N Z J Zool 11(3):259–270

Whitaker AH, Thomas B (1989) New Zealand lizards: an annotated bibliography. Ecology Division, DSIR, Lower Hutt

Wilkes C (1845) Narrative of the United States exploring expedition. During the years 1838, 1839, 1840, 1841, 1842, vol 2. Wiley & Putnam, London

Wilson RA (1949) Late Edgar F. Stead. An appreciation. N Z Bird Notes 3(5):114–115

Winsor MP (1991) Reading the shape of nature: comparative zoology at the Agassiz Museum. University of Chicago Press, Chicago

Womersley HW (1941) New species of *Geckobia* (Acarina: Pterygosomidae) from Australia and New Zealand. Trans R Soc S Aust 65(2):323–328

Woodward TE (1941) Some aspects of the anatomy of *Naultinus elegans*, Gray. MSc dissertation, University of Auckland

Worthy TH (1987) Osteological observations on the larger species of the skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. N Z J Zool 14(2):219–229

Worthy TH (1991) Fossil skink bones from Northland, New Zealand, and description of a new species of *Cyclodina*, Scincidae. J R Soc N Z 21(4):329–348

Worthy TH (2016) A review of the fossil record of New Zealand lizards. Chap. 3. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Wright-St Clair RE (2003) “Historia nunc vivat”. Medical practitioners in New Zealand 1840 to 1930. The author, Hamilton

Yate W (1835) An account of New Zealand and of the Church Missionary Society’s Mission in the Northern Island, 2nd edn. RB Seeley and W Burnside, London

Zug GR (1985) Pacific Island lizards – status of type specimens from the US exploring expedition 1838-1842. Copeia 1985(1):150–154

Chapter 3
A Review of the Fossil Record of New Zealand Lizards

Trevor H. Worthy

Abstract The fossil record of squamates in New Zealand is scant, and this chapter represents the first systematic review of the available information for this reptile group in New Zealand. The oldest fossil squamates are found in the Early Miocene (19–16 mya) St Bathans Fauna. The material represents skinks referred to Eugongylinae similar to extant species of *Oligosoma* and geckos referred to Diplodactylidae, which differ little from extant New Zealand geckos. No other squamates are represented in the St Bathans Fauna. The Early Miocene St Bathans skinks and geckos formed part of a fauna that was similar to the recent prehuman New Zealand fauna as it was dominated by birds and included sphenodontids and leiopelmatid frogs, but differed markedly by the additional presence of a crocodilian, terrestrial turtles and greater mammalian diversity. A squamate fossil record is then unknown until the last 50,000 years of the late Quaternary. This late Pleistocene to Holocene fauna, however, documents the natural, undisrupted biota that was encountered and decimated by humans and the species they introduced. Fossil squamates are relatively common, but little studied. Notably, they document the former widespread presence of a suite of large forms. Among skinks, these include two extinct taxa in the Northland region of North Island, including *Oligosoma northlandi*, the largest skink known from New Zealand. In Northland and elsewhere on the North Island, fossils attest to the more widespread presence of *Oligosoma alani*, *O. whitakeri*, *O. macgregori* and *O. oliveri*. In both North and South Islands, *Hoplodactylus duvaucelii* was widespread. The available information for the kawekaweau (*Hoplodactylus delcourti*) is reviewed, and the lack of fossil evidence for it is discussed.

Keywords Fossil squamates • Scincidae • Diplodactylidae • St Bathans Fauna • Quaternary • New Zealand

---

T.H. Worthy (✉)
School of Biological Sciences, Flinders University of South Australia, Adelaide, SA, Australia
e-mail: trevor.worthy@flinders.edu.au

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_3

3.1 Introduction

New Zealand is well known as the land of birds as they dominate diversity and because ground-dwelling mammals were absent when humans arrived (e.g. Hutton 1874; Hutton and Drummond 1904; Attenborough 1998; Morris and Ballance 2003). There were, however, three bats in the Recent fauna (King et al. 2009). The endemic family Mystacinidae included two species that could forage on the ground, *Mystacina robusta* (possibly extinct) and *M. tuberculata*. The third species, *Chalinolobus tuberculatus*, is of the cosmopolitan Vespertilionidae. The dominance of birds and absence of land mammals have intrigued naturalists since New Zealand first came to the notice of European scientists (e.g. Hutton and Drummond 1904; Andrews 1986; Gibbs 2006). But, the unique nature of New Zealand's fauna does not stop there. The herpetofauna is also depauperate, as was long ago noted by Hutton and Drummond (1904). In terrestrial or freshwater environments, there are no crocodilians or turtles. Among the squamates, major groups are lacking: there are no acrodont (teeth lack roots and are not in sockets) taxa, such as chamaeleons (Chamaeleonidae) and dragons (Agamidae), and no iguanas (Iguanidae). The tuatara reptiles are all one species, *Sphenodon punctatus*: Sphenodontidae (Rhynchocephalia) (Cree 2014). The amphibians are limited to just six species (three extinct, three extant) of frogs (Anura: Leiopelmatidae). This lack of diversity is partly compensated for by the special status of Leiopelmatidae and *Sphenodon*. The former taxon, with *Ascaphus* (Ascaphidae) of North America, is the sister group of remaining Anura (e.g. Pyron and Wiens 2011 and references therein). The latter taxon is the only living member of Rhynchocephalia anywhere in the world, despite this group having equal rank to Squamata and once being diverse and globally distributed (Jones et al. 2009; Meloro and Jones 2012; Apesteguía et al. 2014).

The presence of the relictual taxa *Sphenodon* and *Leiopelma* and the absence of many taxonomic groups have long been attributed to the vicariant origin of the New Zealand fauna and its subsequent long isolated insular nature (e.g. Hutton and Drummond 1904; Fleming 1979; Stevens 1980a, b; Worthy and Holdaway 2002; Wilson 2004; Gibbs 2006). Given this unique faunal composition, it perhaps should come as no surprise that in the land of birds, the largest radiations of vertebrates are not birds, but rather two squamate families—Scincidae and Diplodactylidae. It is only recently that this has been appreciated following a more than 50 % increase in their known diversity since 1980 (Wilson 2004; Hitchmough et al. 2016). Now, Scincidae and Diplodactylidae have 61 and 43 species in New Zealand, respectively, far outnumbering those of any avian family in New Zealand (Hitchmough et al. 2016). This increase in squamate diversity reflects a new appreciation of largely allopatric cryptic morphological diversity revealed by molecular analyses of mitochondrial and nuclear DNA (Hitchmough et al. 2016).

In this chapter, I explore the fossil record of squamates in New Zealand to provide some context for the modern fauna and make an attempt to answer the following questions. Has New Zealand always had the limited herpetofaunal diversity that greeted Europeans (see Shea 2016)? Was it more diverse at familial and ordinal level in the past? What was the impact of the arrival of humans, and the species they introduced just some 750 years ago (see Towns et al. 2016), on the Recent (Holocene) faunas?

It must be noted at the outset that the fossil record of terrestrial vertebrates, including lizards, in most places in the world, such as Europe, the Americas and Australia, is infinitely better than that of New Zealand. There is only one fossil lizard taxon named from New Zealand (Worthy 1991), whereas elsewhere, many taxa, dating back into the Mesozoic, have been described (e.g. Estes 1983; Evans 2003; Martin et al. 2004; Albino and Brizuela 2014; Daza et al. 2014). Even in Australia, where the fossil record of lizards is considered poor (Martin et al. 2004), multiple taxa are described. Scincids, the most diverse Australian lizards, are known by several late Oligocene to Early Miocene fossils (Hutchinson 1992; Martin et al. 2004 and references therein) and gekkotans include an Early Miocene pygopod (Hutchinson 1997). Several extinct taxa have also been described from the Pliocene and Quaternary (e.g. Mackness and Hutchinson 2000; Hutchinson and Mackness 2002; Hutchinson and Scanlon 2009; Čerňanský and Hutchinson 2013).

The poor New Zealand fossil record of squamates is explained in large part by the abysmal record of terrestrial vertebrates from New Zealand generally (Worthy and Holdaway 2002). This is particularly the case if one excludes the late Pleistocene and Holocene (i.e. the last 100,000 years). There is a good marine fossil record for New Zealand in which cetaceans and penguins are numerous. The latter first appear about 63 million years ago [mya] and include a diversity of species sampling all epochs until the present. Unfortunately, the terrestrial vertebrate record is generally non-existent. It begins with a few fragmentary dinosaurs and pterosaurs in marine sediments dating from just before the K–Pg boundary in the latest Mesozoic at about 67–65 mya, most notably in the Hawke's Bay and on the Chatham Islands (Wiffen and Molnar 1988; Molnar and Wiffen 1994; Stilwell et al. 2006). In the early Cenozoic period, two species of volant seabirds (Mayr and Scofield 2014, 2016), dating to 60.5–61.6 mya in the Paleocene epoch, have also recently been reported from the Waipara River Greensands along with the proto penguins, *Waimanu* spp., for which the site is renowned. There is then a 40 mya gap where no terrestrial vertebrate fossils are known.

3.2 St Bathans Fauna: A Miocene Window into New Zealand's Terrestrial Vertebrate Diversity

The St Bathans Fauna offers the first glimpse of the terrestrial fauna on Zealandia (see Chapple and Hitchmough 2016), the partially submerged continent of which New Zealand is a part. This fauna is named after the small village of St Bathans, Central Otago, located near the fossil-bearing deposits (Worthy et al. 2007; Fig. 3.1). The St Bathans Fauna was recovered from lacustrine deposits of the

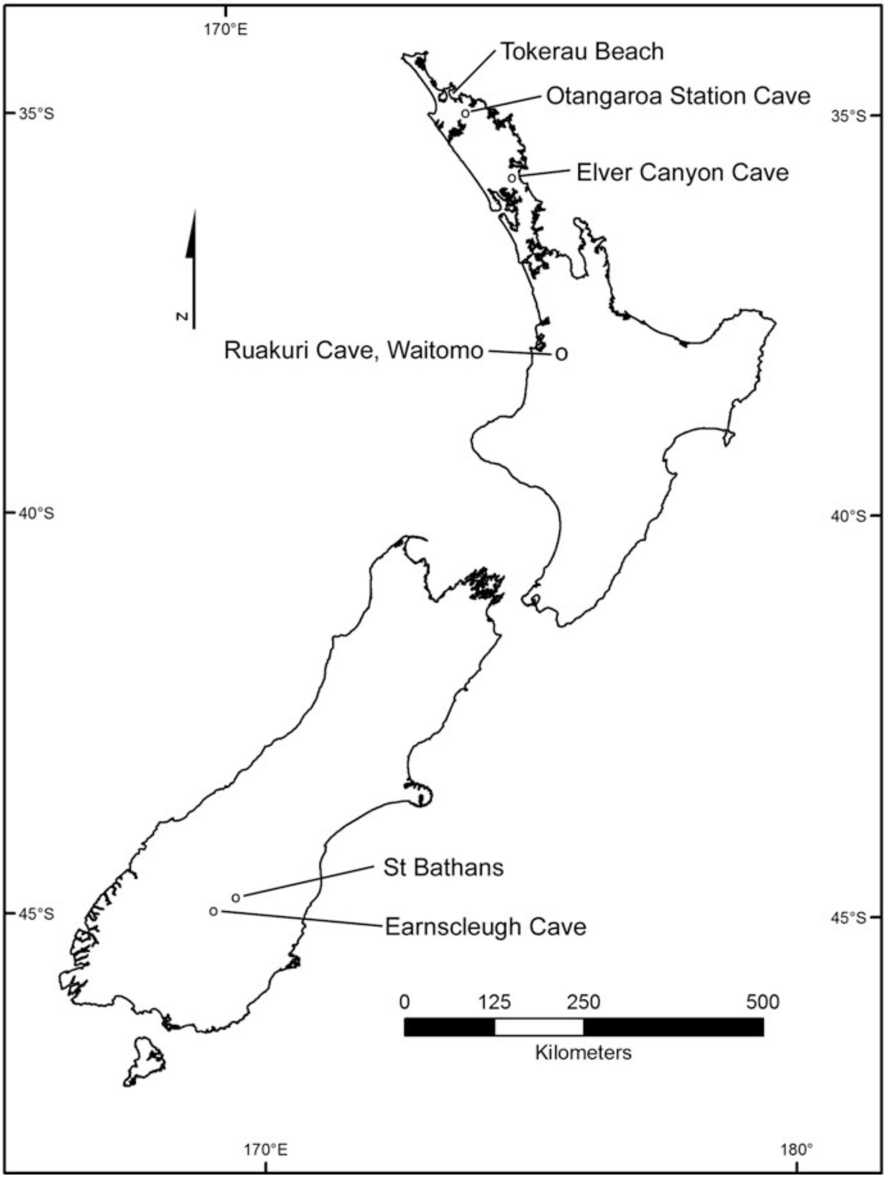


Fig. 3.1 Location of fossil sites containing squamate fossils discussed in the text

Bannockburn Formation that were laid down in the huge (5600 km^2) palaeolake Manuherikia. It is poorly dated but generally considered to be from the Early Miocene in the Burdigalian age, locally known in New Zealand as the Altonian stage (i.e. 16–19 mya old, Mildenhall 1989; Mildenhall and Pocknall 1989; Worthy et al. 2007; Reichgelt et al. 2015). This is a very rich and diverse fauna, with over

7000 terrestrial vertebrate fossil specimens collected since 2000. As the St Bathans Fauna includes the oldest fossil squamates known from New Zealand, it is worth considering this assemblage and the palaeoenvironmental context in which it was deposited.

The environment around this lake was characterised by a subtropical climate that supported a diverse mixed Nothofagaceae—Podocarpaceae forest, which included abundant laurels, palms, podocarps, eucalypts and casuarinas (Mildenhall 1989; Mildenhall and Pocknall 1989; Pole and Douglas 1998; Pole et al. 2003; Hand et al. 2015). This environment has been said to be similar to that of modern day New Caledonia or southeast Queensland in Australia (Reichgelt et al. 2015), so it was much warmer than the present-day Otago.

As of 2016, some 40 species of birds, comprising a diverse range of families (e.g. Tennyson et al. 2010; Scofield et al. 2010; Worthy et al. 2007, 2010, 2011a, 2013a, b; De Pietri et al. 2015 and references therein; see Table 3.1), five bat taxa and a couple of undescribed rare and enigmatic terrestrial-type mammals (Worthy et al. 2006; Hand et al. 2015; and unpubl. data) are known from the St Bathans Fauna. Associated with fossils of these birds and mammals are those of several herpetofaunal species that attest to a greater familial diversity in the Early Miocene than that found in New Zealand at present. These include those of an as yet undescribed crocodilian; a large undescribed terrestrial turtle (?Meiolanidae), perhaps related to the horned meiolanids known from Lord Howe Island, New Caledonia and Australia, and leiopelmatid frogs (Leiopelmatidae: a large species *Leiopelma miocaenale* and a small species *L. acricarina*) (Worthy et al. 2011b, 2013c). Some squamate fossils (Lee et al. 2009) and rare rhychocephalian fossils classified as Sphenodontidae: Sphenodontinae, which possess dentition very similar to that of the modern *Sphenodon punctatus* (tuatara), have also been recorded as part of the St Bathans Fauna (Jones et al. 2009).

The squamates are a relatively common component of the St Bathans Fauna, with about 230 specimens known in 2016. However, all are single bones and are generally broken. Despite other squamate taxa in the world being named from similar incomplete specimens (e.g. Daza et al. 2014), Lee et al. (2009) did not name any of these fossils because individual fragments rarely provide sufficient detail to identify taxonomic relationships. Moreover, association of elements to one of the two or more species present could not be justified. Furthermore, osteological variation among New Zealand lizards, and arguably lizards in general (see Bell and Mead 2014), remains poorly known so that phylogenetic inferences made from single elements cannot be considered reliable. Also, interim observations suggest that many living taxa are osteologically cryptic, and it is unknown which, if any, individual bones can provide morphological characteristics that might distinguish between the ~61 *Oligosoma* species or the 43 New Zealand diplodactylids. Nevertheless, Lee et al. (2009) were able to establish that both skinks and geckos are represented in the St Bathans Fauna, and that based on size, there was at least a large and a small species of each group present (Figs. 3.2 and 3.3). The most significant aspect of this finding is that these lizard fossils represent essentially the same groups as those found in present-day New Zealand: *Oligosoma*

Table 3.1 A list of terrestrial vertebrates recorded from the Early Miocene St Bathans Fauna showing the taxa found with the skinks and geckos

Higher taxon	Genus	Species	Common names
Amphibia			
Leiopelmatidae	*Leiopelma*	*miocaenale*	New Zealand frogs
		acricarina	
Non-avian Reptilia			
Crocodilia	Genus indet.	n. sp. 1	Crocodilian
?Meiolanidae	Genus indet.	1 indet. sp.	?Horned tortoise
Sphenodontidae	cf. *Sphenodon*	1 indet. sp.	Tuatara
Scincidae	Genus indet. cf. *Oligosoma*	2 indet. spp.	Skinks
Diplodactylidae	Genus indet. cf. *Hoplodactylus*	2 indet. spp.	Geckos
Mammalia			
Mystacinidae	*Mystacina*	*miocenalis*	St Bathans burrowing bat
		n. sp. 2	Indet. sp. burrowing bat
		n. sp. 3	Indet. sp. burrowing bat
Microbat: fam. nov.	Genus indet.	n. sp. 1	Undescribed microbats
Vespertilionidae	Genus indet.	n. sp. 1	Indet. microbats
Microbat: family indet.	Genus indet.	n. sp. 1	
Order and family indet.	Genus indet.	1 indet. sp.	Terrestrial mammals indet.
Aves			
Dinornithiformes	Genus indet.	sp. indet.	Moa
Apterygiformes	*Proapteryx*	*micromeros*	St Bathans kiwi
Pelecanoididae	*Pelecanoides*	*miokuaka*	Miocene diving petrel
Anatidae	*Manuherikia*	*lacustrina*	Manuherikia duck
		minuta	Minute Manuherikia duck
		douglasi	Douglas' duck
		n. sp.	Undescribed sp.
	Miotadorna	*sanctibathansi*	St Bathans shelduck
	Dunstanetta	*johnstoneorum*	Johnstones' duck
	Matanas	*enrighti*	Enright's duck
Anserinae	cf *Cereopsis*	sp. indet. 1	Goose cf Cape Barren Goose
		sp. indet. 2	Indet. goose
Palaelodidae	*Palaelodus*	*aotearoa*	New Zealand palaelodus
Accipitridae	Eagle: genus indet.	n. sp. 1	Undet. eagle
	Kite: genus indet.	n. sp. 2	Undet. hawk
Ardeidae	*Matuku*	*otagense*	St Bathans heron

(continued)

Table 3.1 (continued)

Higher taxon	Genus	Species	Common names
	Pikaihao	*bartlei*	Bartle's bittern
Aptornithidae	*?Aptornis*	*proasciarostratus*	St Bathans adzebill
Rallidae	Genus indet.	n. sp. 1	Undet. rails
		n. sp. 2	
Charadriiformes	Genus indet.	n. sp. 1	Gull
	Hakawai	*melvillei*	New Zealand lake wanderer
	Small waders: genus indet.	n. sp. 1—laricola-like	Gull-like bird
	Small waders: genus indet.	n. sp. 1—charadriid	Dotterel-like bird
		n. sp. 2—charadriid	Dotterel-like bird
Columbidae	*Rupephaps*	*taketake*	St Bathans pigeon
	Genus indet.	n. sp. 1	St Bathans dove
Strigopidae	*Nelepsittacus*	*minimus*	Little St Bathans parrot
		donmertoni	Merton's parrot
		daphneleeae	Lee's parrot
	Genus indet.	n. sp. 1	Large indet. parrot
Aegothelidae	*Aegotheles*	n. sp.	Owlet nightjar
Apodidae	*Collocalia*	sp. indet.	Swiftlet
Aves Fam. Nov.	Genus indet.	n. sp.	Unknown
Passeriformes			
Acanthisittidae	*Kuiornis*	*indicator*	St Bathans wren
Cracticidae?	Genus indet.	n. sp. 1	Undetermined
Family Indet.	Genus indet.	n. spp. 2–5	Undetermined

(Eugongylinae) skinks and Diplodactylidae geckos (Hitchmough et al. 2016). In 2009, when Lee et al. (2009) analysed these fossils, New Zealand geckos were classified in just two genera (*Naultinus* and *Hoplodactylus*). The fossil gecko bones were identified as similar to those of *Hoplodactylus* because the frontal bones were more similar to those of *Hoplodactylus* species than the much shorter form of *Naultinus* species. Since then, *Hoplodactylus* has been split into multiple genera (Nielsen et al. 2011, see Hitchmough et al. 2016), and *Naultinus* found to be monophyletic but embedded within the radiation of *Hoplodactylus* species. So if one assumes the morphology of *Hoplodactylus* frontal bones is plesiomorphic (i.e. the ancestral form) and that of *Naultinus* derived (i.e. from the plesiomorphic form), then the fossils may represent the plesiomorphic state. However, Daza et al. (2014) considered the fossils to be more similar to *Woodworthia maculata* than to *Hoplodactylus duvaucelii* based on characteristics of the frontal, compound bone and pterygoid. If so, this may suggest that the fossils are from a crown-group taxon. This suggestion is consistent with analyses of molecular data that suggest the New Zealand geckos split from their Australian sister relatives at about 40.2 mya,

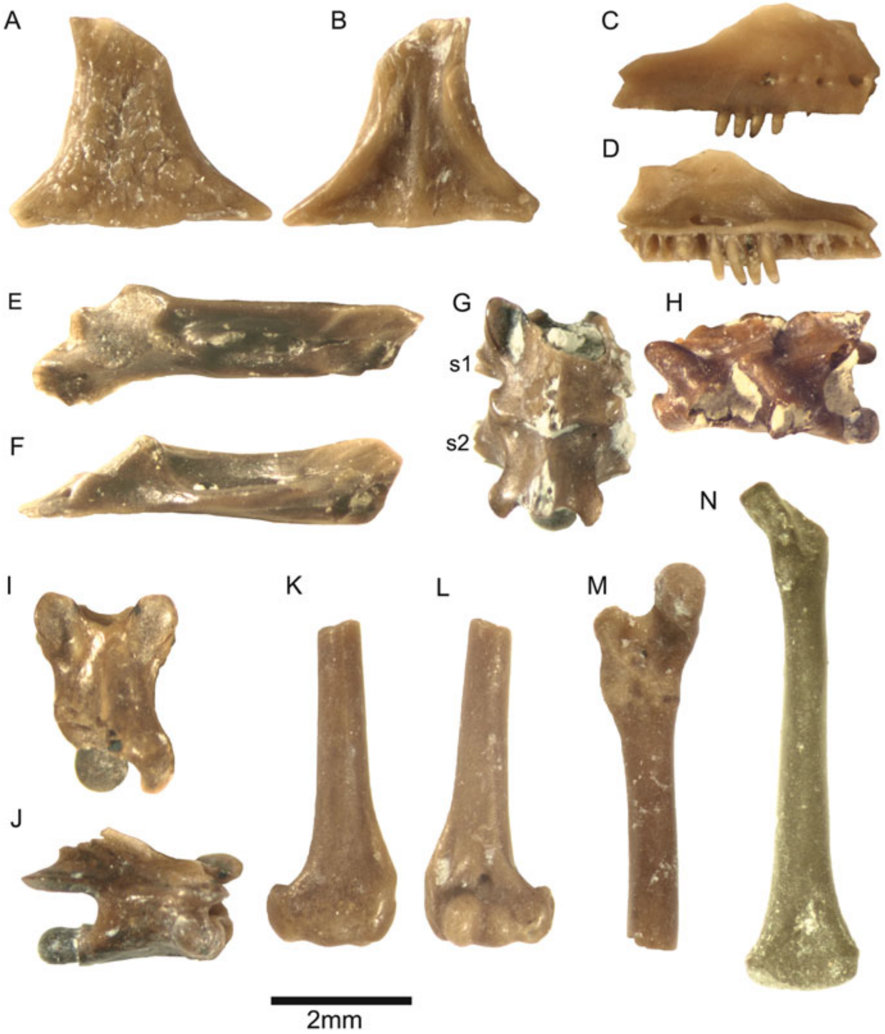


Fig. 3.2 Bones of skinks (Scincidae: Eugongylinae) from the St Bathans Fauna, Bannockburn Formation, Manuherikia Group, New Zealand, Early Miocene 19–16 Ma. (**a**) Dorsal and (**b**) ventral view of frontal bone NMNZ S42688. (**c**) Lateral and (**d**) medial view of right maxilla S44218. (**e**) Dorsal and (**f**) medial view of right compound lower jaw element S42689. (**g**) Dorsal and (**h**) left lateral view of sacral vertebrae S50708 with the first (s1) and second (s2) vertebrae indicated. (**i**) Dorsal and (**j**) right lateral view of dorsal vertebra S50708. (**k**) Dorsal and (**l**) ventral view of distal end of right humerus S44002. (**m**) Posterior and (**n**) ventral view of right femur S50945 and S50810, respectively. Modified from Lee et al. (2009)

and the age of the New Zealand crown group is about 24.4 mya (Nielsen et al. 2011), some five or more mya older than to the deposition event of the St Bathans fossils.

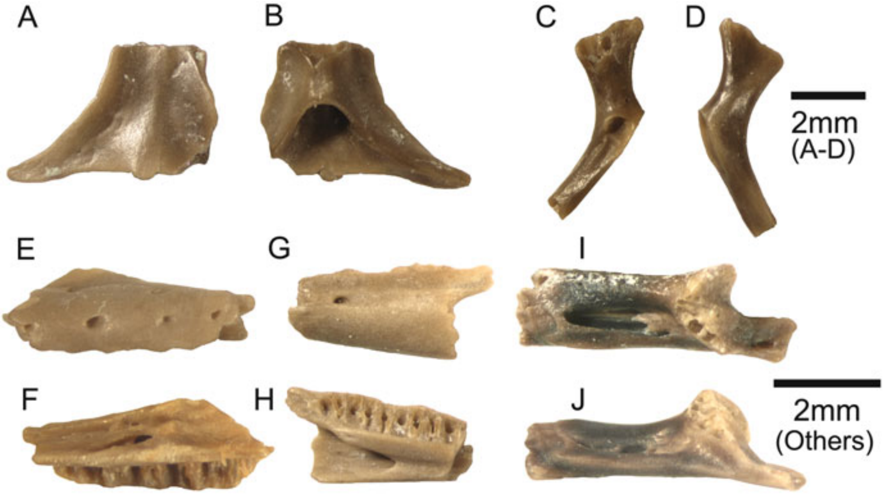


Fig. 3.3 Gekkotan material from the St Bathans Fauna. (**a**) Dorsal and (**b**) ventral view of frontal NMNZ S43124. (**c**) Lateral and (**d**) medial view of right left pterygoid S44154. (**e**) Lateral and (**f**) medial view of left maxilla S51004. (**g**) Lateral and (**h**) medial view of left dentary S42296. (**i**) Dorsal and (**j**) medial view of right compound bone of lower jaw S44338. Modified from Lee et al. (2009)

Analyses of molecular data for New Zealand skinks (Chapple et al. 2009) suggest that skinks colonised New Zealand in the Early Miocene (22.6–16 mya): a similar or slightly more recent time frame to the geckos. The St Bathans fossil skinks may therefore represent some of the earliest members of the New Zealand group. About 17.5 mya, as New Zealand skinks radiated from their Australian counterparts, a deep, major split occurred. This split separates clades 1 + 2 on the South Island from clades 3–5 on the North Island. This is in accordance with latest palaeogeographic reconstructions (e.g. see GNS website [http://www.gns.cri.nz/Home/Our-Science/Energy-Resources/Oil-and-Gas/NZs-Sedimentary-Basins/Paleogeographic-maps]; Peter Kamp pers. comm. 20 Jan 2016; Fig. 3.4) that show that two main land masses existed during the Oligocene and into the Early Miocene—a smaller one whose rocks are now in Northland and a second larger, more southern one whose rocks are now preserved in the Taranaki and Otago region (Fig. 3.4; Kamp et al. 2014; Strogen et al. 2014). So these clades may reflect initial radiations on each of these land masses. To test these inferences from molecular data, a fossil site with the capacity to preserve squamates from rocks a few million years older than those revealing the St Bathans Fauna is sorely needed—something from the Oligocene about 30–24 mya would be most instructive.

To summarise, more than 7000 terrestrial vertebrate fossils have so far revealed about 230 skink and gecko bones from the Early Miocene St Bathans Fauna. Given these numbers, it seems most unlikely that any other squamate families were represented in the New Zealand terrestrial fauna at that time. If so, it seems that lizards, such as Agamidae and Varanidae, and snakes (e.g. Pythonidae,

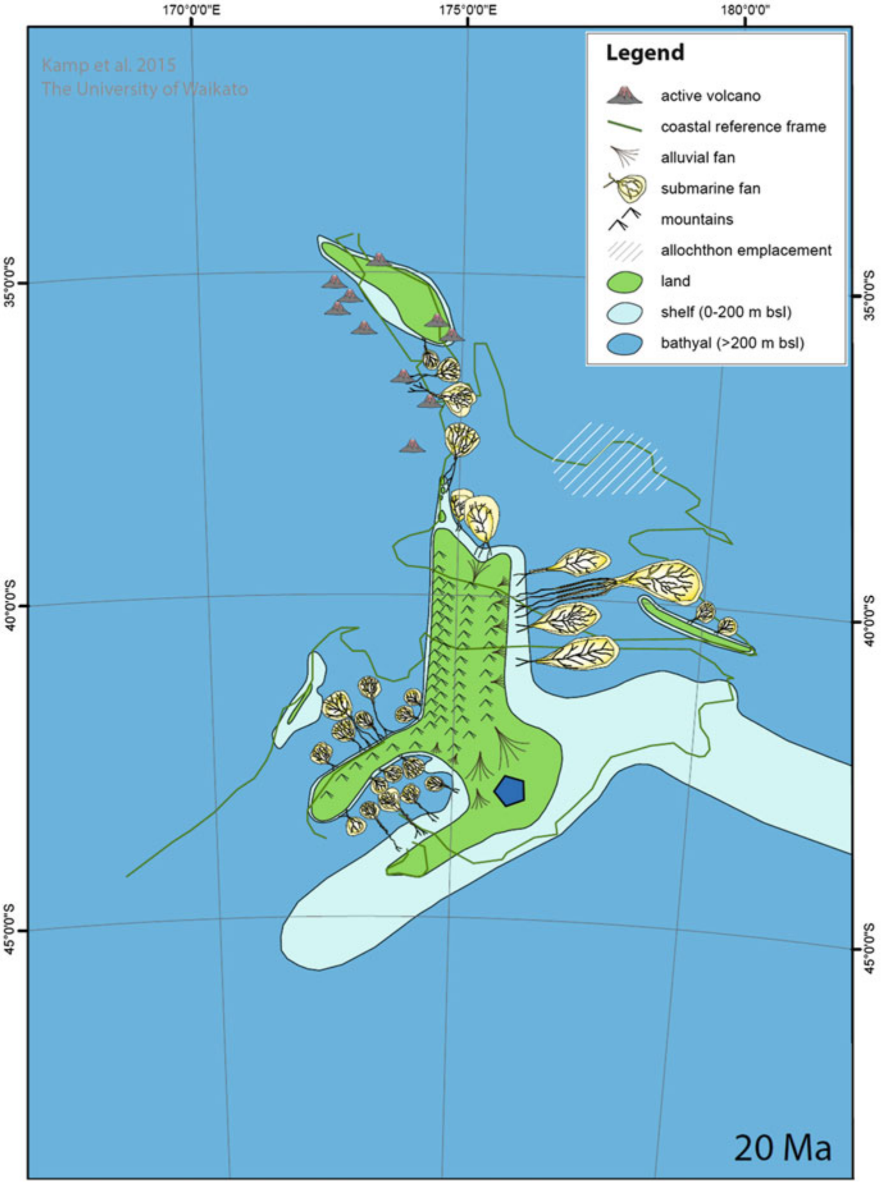


Fig. 3.4 A palaeogeographic reconstruction showing land on Zealandia in the New Zealand region at 20 mya. The *polygon* marks the location of Lake Manuherikia. Map provided by Peter Kamp, University of Waikato, 2016

Typhlopidae, Elapidae) were absent despite their diverse presence in the closest land mass of Australia.

3.3 Quaternary Fauna: An Insight into the Biodiversity Impacted by Humans

After deposition of the St Bathans Fauna in the Early Miocene, the New Zealand record is again blank for the next 16 mya until the Pleistocene. Then in late Pleistocene and Holocene deposits, a rich and well-known record for birds, bats and tuatara documents the immediate prehuman biota (e.g. Worthy and Holdaway 2002 and references therein). Fossils of lizards are also present, but have attracted much less attention due to the small size of the bones, the cryptic nature of the represented taxa and the poorly resolved nature of New Zealand lizard taxonomy. There are still many undescribed living species (particularly for the geckos; see Hitchmough et al. 2016).

3.3.1 Evidence for Large Forms in the Holocene Fauna

Lizard bones have been often reported from fossil and archaeological faunas from New Zealand (e.g. Gill 1985; Worthy 1987a, 1991 and references therein). However, most have not been identified to species level. The principle focus has been on the evidence for large taxa, those that are approximately equal to the largest, or larger than, lizards currently surviving on the mainland. Gill (1985) demonstrated that a skink existed on Motutapu Island until Maori colonisation. At a snout-vent length (SVL) of ~155 mm, this skink was as large as, or larger than, the largest skink species known from New Zealand's offshore islands (see Cree and Hare 2016).

Worthy (1987a, 1991) found that adults of *Oligosoma alani* (as *Cyclodina alani*), *O. oliveri* (as *C. oliveri*), *O. whitakeri* (as *C. whitakeri*) and *O. macgregori* (as *C. macgregori*) could be separated from all smaller taxa (then identified as *Leiolopisma* species) by various features of skull bones. These include the dentary, where the lower caudal notch ends caudal to the upper notch; the braincase (occipital capsule), which has a well-developed ridge marking only the anterior end of the prootic-supraoccipital suture (in species then listed in *Leiolopisma*, it extends over the whole suture) and the quadrate, which has a pronounced anteromedial ridge arising dorsally and aligned vertically and is widest at about mid-height (quadrates in species of *Leiolopisma* lack the anteromedial ridge and are widest in the dorsal third of height). Interspecific variation in these elements, and in the frontal, parietal and maxilla, allowed Worthy (1987a) to identify fossils preserving these elements. The main finding was that there were large fossil skinks

Fig. 3.5 A fossil skeleton of *Oligosoma alani* from Hilltop Cave in the Waitomo Caves Museum (cat. number WCM 11655). Image courtesy of Waitomo Caves Museum

widely distributed on the North Island, but not in the South Island, during the Holocene and that these were not restricted to offshore islands during this period. The most abundant and widespread fossil form was identified as the largest known extant species, *O. alani* (as *Cyclodina alani*), e.g. the specimen shown in Fig. 3.5, with no larger species being represented by fossils south of Auckland. *Oligosoma macgregori* (as *Cyclodina macgregori*) and *O. whitakeri* (as *C. whitakeri*) were identified from sites in Northland and the Waitomo region, and *O. oliveri* (as *C. oliveri*) only from Otangaroa Station Cave in Northland.

However, a remarkable discovery in Rimrock Passage in Ruakuri Cave, Waitomo in 1998 revealed a rich collection of fossil frogs and lizards and that all four large '*Cyclodina*' species, which were then recognised, were in the Waitomo region in the late Holocene. I was lucky enough to visit this passage and to identify and collect specimens for the Waitomo Caves Museum. Along with 18 individual skeletons of the giant extinct frog *Leiopelma waitomoensis*, there were eight *L. markhami*, two *L. archeyi* (the first and only fossils of this taxon identified at Waitomo), two *Oligosoma alani*, two *Oligosoma ornatum* and ten *Oligosoma* sp. cf. *O. oliveri* (Fig. 3.6). These specimens await formal appraisal of their identity.

Given that all of these species of large extant '*Cyclodina*' skinks are now listed in *Oligosoma* along with all other New Zealand skinks (Chapple et al. 2009; Hitchmough et al. 2016) and that some of these large taxa as then defined, e.g. *C. oliveri*, are now split into more than one allopatric species, what can be taken from Worthy's (1987a) identifications? Firstly, the variation detected in the specimens that Worthy (1987a) compared shows that there is the promise of osteological identification of the fossil material—but this needs to be re-examined in the context of current nomenclature. The four large '*Cyclodina*' species are all now included in clade 4 with *Oligosoma fallai*. Skeletons of this latter species were not available to Worthy (1987a), so if it shares the above features with the former 'Cyclodina' species, then they may characterise this clade.

Fig. 3.6 An articulated fossil skeleton of a skink, provisionally identified as *Oligosoma oliveri*, found in Rimrock Passage, Ruakuri Cave, Waitomo in 1998, now WCM 15278. The skull is about 13 mm wide. Photograph by Trevor H. Worthy

Alternatively, these features, which likely all relate to the jaw architecture, may be related to large size and robustness of these species.

Only one extinct species of skink has been described to date from fossils from New Zealand. This is *Cyclodina northlandi* (Worthy, 1991) (Fig 3.7), which is now listed as *Oligosoma northlandi* (Worthy, 1991), see Chapple et al. (2009) and Hitchmough et al. (2016). It was based on bones from two caves, Otangaroa Station Cave and Elver Canyon Cave, both in Northland, where it co-occurred with *O. alani*. It was diagnosed as a large species of *Cyclodina,* with adults larger than all congeners: its femora are 30 % longer than those of the largest known fossil femora and 50 % longer than those in the available recent skeletons of *O. alani*; it has 33 dentary teeth or alveoli and 25 or 26 maxillary teeth; the quadrate is widest in the dorsal third of height; and the caudal notches on the dentary are of equal depth. This contrasts with *O. alani*, the closest species in size, which has 26–29 dentary teeth, 23 maxillary teeth, quadrates that are widest at mid-height and a dentary in which the lower caudal notch is always shallower. The latter two features have been said to characterise all other '*Cyclodina*' species. Based on body proportions of *O. alani*, the SVL of *O. northlandi* can be estimated as 235 mm with a total length of perhaps 400–500 mm, a truly giant skink relative to living New Zealand forms: nearly twice as large as the largest living adult species (*Oligosoma alani*; maximum 140 SVL).

Worthy (1991) also reported that a large skink is represented in the sand dune deposits at Tokerau Beach in the Far North. It was similar in size to *Oligosoma* (*Cyclodina*) *alani* and *O. northlandi* and thus much larger than most other known taxa, but was considered to belong to a species in the genus *Leiolopisma* (now *Oligosoma*). This was because the ventral notch is deeper than the dorsal notch in the dentary, not shallower as in *Cyclodina*, and because it has 28–31 dentary teeth, a number intermediate between the counts for *O. alani* and *O. northlandi*. The only

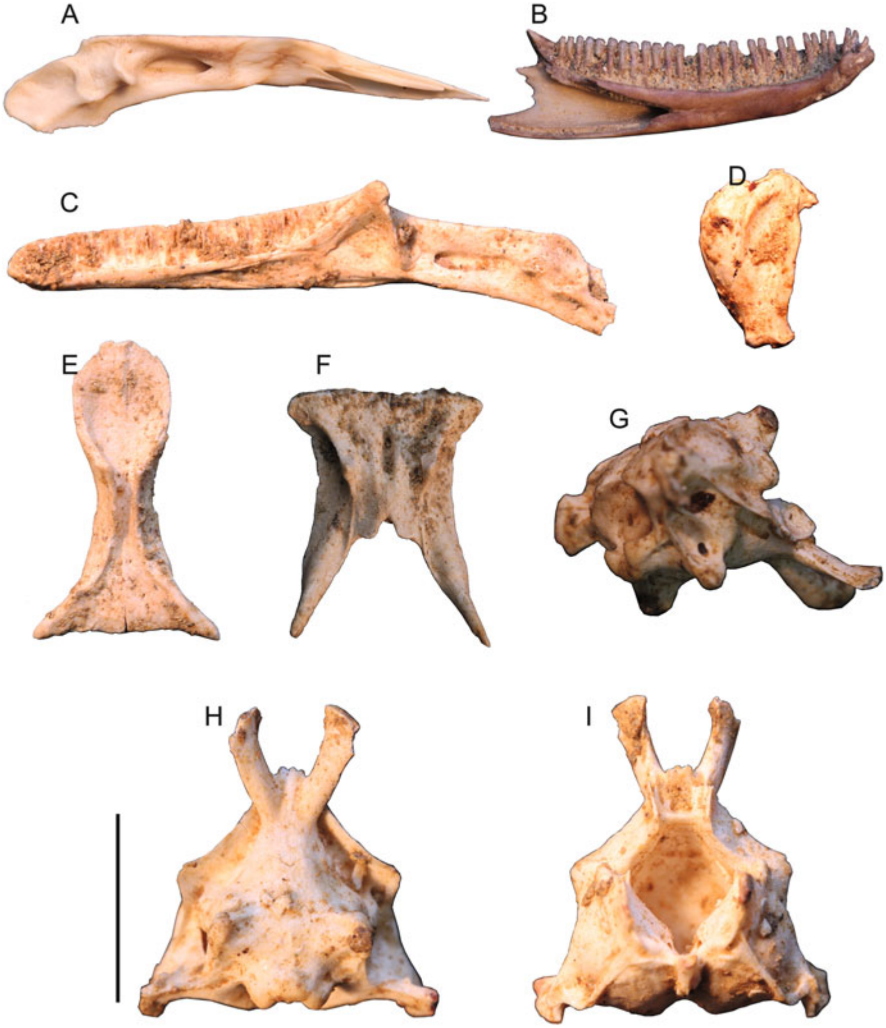


Fig. 3.7 Fossil bones of *Oligosoma northlandi*. (**a**) Dorsomedial view left compound bone, (**b**) medial view left dentary, paratype, WCM 28324 (WO371), Paryphanta Passage, Elver Canyon Cave, Waipu; (**c**) right lower jaw, (**d**) anterior view right quadrate, (**e**) ventral view frontal, (**f**) ventral view parietal, Holotype, WCM 28322 (WO332.1), Otangaroa Station Cave, Northland; (**g**) right lateral, (**h**) ventral, and (**i**) dorsal view of braincase, paratype, WCM 28323 (WO332.5), Otangaroa Station Cave. Scale bar is 10 mm. Image prepared by author from photographs provided courtesy of Waitomo Caves Museum

species of similar size are *O. fallai* from the Three Kings and *O. homalonotum* from Great Barrier and Little Barrier Islands. It is unlikely to be *O. fallai*, which is endemic to the Three Kings Islands where most plants and animals are either endemic or deeply divergent from relatives in Northland. However, the isolation of *O. homalonotum* on Great Barrier and Little Barrier Islands is likely to reflect stranding following rising sea level in the Holocene and subsequent extinction on Northland. Skeletons of these species were unavailable to Worthy in 1990 to make direct comparisons, and so the affinity of this large skink remains unknown.

Regardless, these data show that at least one novel giant skink was present in Northland, that two other large taxa existed on the mainland of Northland in prehuman times (*O. alani* and perhaps *O. homalonotum*) and that, along with *O. alani,* the other large taxa now restricted to islands (*O. oliveri, O. macgregori*), or islands plus a tiny southern North Island refuge (*O. whitakeri*), were more widespread on the North Island (see Chapple and Hitchmough 2016). None of these taxa have been identified from South Island deposits, supporting the theory that this clade was restricted to the North Island. However, as was long ago acknowledged (Whitaker 1978; Towns 1985), the current distribution of these taxa is undoubtedly relictual and of recent origin. It can be attributed to predation by the Pacific rat *Rattus exulans*, which was introduced to New Zealand about 750 years ago (e.g. Wilmshurst et al. 2008; Towns et al. 2016). The largest skinks were the most affected by predation, much like the native *Leiopelma* frogs, of which the three largest taxa also went extinct at this time (Worthy 1987b).

Along with those of skinks, gecko bones of a size appropriate for the *Hoplodactylus duvaucelii* are widely distributed on the North Island where they range from Northland to Martinborough (Worthy 1987a). On the South Island, similar bones have been recovered from Northwest Nelson (Worthy and Holdaway 1994), North Canterbury (Worthy and Holdaway 1995, 1996), South Canterbury (Worthy 1997) and Otago (Worthy 1998). This contrasts with the current range of this species, which is now generally restricted to islands, although a relict population has recently been found in the Waikato (Chapple and Hitchmough 2016).

3.3.2 **Hoplodactylus delcourti***: A Stuffed Relic from Colonial Explorations and the World's Largest Gecko*

One of the enduring mysteries of New Zealand herpetology, and indeed of that for geckos globally, is the identity and origin of a specimen held in the Musée d'Histoire Naturelle de Marseille, France. This specimen is a stuffed skin of a giant gecko (Fig. 3.8). With an SVL of 370 mm and a total length of 622 mm, it is 54 % larger than the previous largest known gecko and so of global interest to gecko biologists. The skin was diagnosed as from a species of carphodactyline gecko based on the arrangement of preanal pores, and the subparallel tightly bound third and fourth metatarsals. Based on digital morphology, it was referred to the genus *Hoplodactylus* and described as the new species *H. delcourti* Bauer and Russell 1986 (Bauer and Russell 1986, 1987). It is 134 % larger than the largest known specimen of *Hoplodactylus duvaucelii*, the largest New Zealand gecko. Bauer and Russell (1986, 1987) raised the possibility that it may be the kawekaweau of Maori

Fig. 3.8 Images of the holotype of *Hoplodactylus delcourti* in dorsal, right lateral and ventral views. Scale bar is 200 mm. Image prepared from photographs taken by Jan Nauta in 1990 (MA_B.020139; MA_B.020143; MA_B.020145; copyright Museum of New Zealand Te Papa Tongarewa)

legend (also see Shea 2016). However, does this specimen represent a record of a lost New Zealand giant or is it a misplaced specimen: is *Hoplodactylus delcourti* the kawekaweau? Is it solid evidence for a legend? Like a sloughed skin, it reveals the former presence of a lizard now gone. But from where? This single overstuffed skin was discovered, yet forgotten, in the bowels of the Musée d'Histoire Naturelle de Marseille, but it lacks all collection information (Bauer and Russell 1987). To date, investigations into this unique specimen have ranged from delving into museum archives to literally probing the stuffing within it, but these have failed to yield information on a source. Its diagnosis as a species of *Hoplodactylus* suggests that it originates from New Zealand because the genus, as then defined, is restricted to New Zealand, with the nearest relatives in New Caledonia. The specimen was temporarily brought to New Zealand in 1990 as the centrepiece of the 'Forgotten Fauna—New Zealand's Amphibians and Reptiles' exhibition (Bauer and Russell 1990).

The kawekaweau of Maori folklore appears to refer to a large arboreal lizard, alternatively striped longitudinally with dull red or banded with reddish colour, from eastern North Island, though other contenders have been reported from Northland (Bauer and Russell 1987). However, when Bauer and Russell (1986, 1987) related *H. delcourti* to the kawekaweau, *Oligosoma northlandi* and the other similarly gigantic skinks had not been reported, and these taxa are surely good contenders for the source of the kawekaweau. Bauer and Russell (1988) marshalled some osteological evidence for the former existence of giant geckos in New Zealand. Foremost was a report of a jaw found with tuatara bones in Earnscleugh Cave in Otago (Hutton 1875), with spaces for teeth to be attached to the side of the jaw bone (pleurodonty) rather than to the crest of the jaw bone without roots (acrodonty). Hutton recalled some 22 years later that the size of this jaw was about the size of that of a tuatara (Hutton 1899). Pleurodonty—where teeth are in sockets—typifies jaws of most squamates (including skinks and geckos) and differs markedly from the acrodont teeth of tuatara. Unfortunately, no such pleurodont jaw has survived in the collections of Otago or Canterbury Museums, where the fossils from this cave are preserved. Hutton (1899) also described a 14 mm long rib-like bone and raised the possibility that it may have been a rib of the same animal from which the lost jaw derived. Bauer and Russell (1988) argued that this specimen (now in the Canterbury Museum; CM Rep 45) could be a cloacal bone of a gecko and that its size was appropriate for that of *H. delcourti*. However, they did not consider whether this element could be the vestigial rib of a tuatara, whose bones represent at least four individuals in collections from the cave. Nor was much consideration given to the possibility that it may have been a vestigial rib of either a bird, bat or rat. Thousands of bones have been recovered from the cave (Worthy 1998), and no bones of giant squamates are known from this site. Given that geckos have many vertebrae and that these as well as the leg and skull bones would all be easily identified and not overlooked, it appears that no giant gecko was ever present in New Zealand. A femur of a size appropriate for *Oligosoma otagense* is present in the collections, raising the possibility that the large missing pleurodont jaw belonged to a large skink.

As noted by Worthy and Holdaway (2002), there are now many thousands of fossil bones sampling palaeofaunas of all regions of New Zealand, including sites accumulated by predation by owls, falcons and other raptors, by pitfall into caves and which accumulated in sand dunes, swamps or lakes. The remains of many herpetofaunal species have been recovered from these sites in virtually all areas of New Zealand. Bones of tuatara are abundant and widespread. Not one bone of a gecko similar in size to a tuatara, as would be those of *H. delcourti*, has been found. But bones of a gecko the size of *H. duvaucelii*, New Zealand's largest extant gecko species, and of giant skinks, some much larger than any extant species, are widespread. Therefore, if *H. delcourti* did derive from New Zealand, it must have existed in very localised habitats that have not yet been explored by palaeontologists. More likely, it was not a New Zealand animal and originates from a small island in New Caledonia, where other members of the group exist (Nielsen et al. 2011; Bauer et al. 2012).

3.4 Conclusion

The fossil record of terrestrial vertebrates in New Zealand is very poor, with the exception of two small windows in time: the first in the Early Miocene (St Bathans Fauna) and the second in the latest Pleistocene and Holocene periods. The St Bathans Fauna indicates that skinks and geckos similar to those of extant fauna were in New Zealand at that time (19–16 mya) and were likely not accompanied by any other terrestrial squamates—no snakes, agamids or iguanids. The age of these fossils corresponds with the available molecular estimates, but although common, they consist of isolated and fragmentary elements. Establishing whether the fossil species were crown- or stem-group taxa is problematic. The late Pleistocene–Holocene record is much richer but has been little studied. Until now, the poorly known taxonomy of extant fauna and absence of comparative skeletal material have hampered understanding. However, there are now robust taxonomic hypotheses based on molecular data that provide a framework in which to examine the osteology, and, with micro-CT techniques and shape analyses now routine, investigating the fossil resource will be more revealing. We can look forward to assessing with more rigour the identity and relationships of the giant skinks of the North Island. The improvements in recent years in ancient DNA technology make it probable that at least some of the fossils will be amenable to molecular analyses. This would be especially so for those from colder locations, such as the subalpine zone, e.g. Mt Owen in Northwest Nelson, where fossils of indeterminate large taxa are known from and are in collections. Also, the recent nature of the extinctions, all less than 1000 years ago, increases the likelihood of successfully extracting ancient DNA as some fossils may still contain sufficient preserved DNA. To conclude, these factors mean that palaeoherpetology in New Zealand is poised on the verge of a new wave of information and associated knowledge.

References

Albino AM, Brizuela S (2014) An overview of the South American fossil squamates. Anat Rec 297(3):349–368. doi:10.1002/ar.22858

Andrews JRH (1986) The southern ark: zoological discoveries in New Zealand 1769-1900. Century Hutchinson, Auckland

Apesteguía S, Gómez RO, Rougier GW (2014) The youngest South American rhynchocephalian, a survivor of the K/Pg extinction. Proc R Soc B 281:20140811

Attenborough D (1998). The life of birds. David Attenborough Productions, BBC Books

Bauer AM, Russell AP (1986) *Hoplodactylus delcourti* n. sp. (Reptilia: Gekkonidae), the largest known gecko. N Z J Zool 13:141–148

Bauer AM, Russell AP (1987) *Hoplodactylus delcourti* (Reptilia: Gekkonidae), and the kawekaweau of Maori folklore. J Ethnobiol 7:83–91

Bauer AM, Russell AP (1988) Osteological evidence for the prior occurrence of a giant gecko in Otago, New Zealand. Cryptozoology 7:22–37

Bauer AM, Russell AP (1990) Recent advances in the search for the living giant gecko of New Zealand. Cryptozoology 9:66–73

Bauer AM, Jackman TR, Sadlier RA, Whitaker AH (2012) Revision of the giant geckos of New Caledonia (Reptilia: Diplodactylidae: *Rhacodactylus*). Zootaxa 3404:1–52

Bell CJ, Mead JI (2014) Not enough skeletons in the closet: collections-based anatomical research in an age of conservation conscience. Anat Rec 297:344–348

Čerňanský A, Hutchinson MN (2013) A new large fossil species of *Tiliqua* (Squamata; Scincidae) from the Pliocene of the Wellington Caves (New South Wales, Australia). Alcheringa 37:131–136. doi:10.1080/03115518.2012.715326

Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). Mol Phylogenet Evol 52:470–487

Cree A (2014) Tuatara: biology and conservation of a venerable survivor. Canterbury University Press, Christchurch

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Daza JD, Bauer AM, Snively ED (2014) On the fossil record of the Gekkota. Anat Rec 297 (3):433–462. doi:10.1002/ar.22856

De Pietri VL, Scofield RP, Tennyson AJD, Hand SJ, Worthy TH (2015) Wading a lost southern connection: Miocene fossils from New Zealand reveal a new lineage of shorebirds (Charadriiformes) linking Gondwanan avifaunas. J Syst Palaeontol. doi:10.1080/14772019.2015.1087064

Estes R (1983) Handbuch der Palaoherpetologie—Sauria terrestria, Amphisbaenia. Gustav Fischer, Stuttgart

Evans SE (2003) At the feet of the dinosaurs: the origin, evolution and early diversification of squamate reptiles (Lepidosauria: Diapsida). Biol Rev 78:513–551. doi:10.1017/S1464793103006134

Fleming CA (1979) The geological history of New Zealand and its life. Auckland University Press and Oxford University Press, Auckland/Oxford, 141p

Gibb G (2006) Ghosts of Gondwana. The history of life in New Zealand. Craig Potten, Nelson

Gill BJ (1985) Subfossil bones of a large skink (Reptilia: Lacertilia) from Motutapu Island, New Zealand. Rec Auckland Inst Mus 22:69–76

Hand SJ, Lee DE, Worthy TH, Archer M, Worthy JP, Tennyson AJD, Salisbury SW, Scofield RP, Mildenhall DC, Kennedy EM, Lindqvist JK (2015) Miocene fossils reveal ancient roots for New Zealand's endemic *Mystacina* (Chiroptera) and its rainforest habitat. PLoS One 10(6): e0128871. doi:10.1371/journal.pone.0128871

Hitchmough RA, Patterson GB, Chapple DG (2016) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hutchinson MN (1992) Origins of the Australian scincid lizards: a preliminary report on the skinks of Riversleigh. Beagle Rec North Territory Mus Arts Sci 9:61–70

Hutchinson MN (1997) The first fossil pygopod (Squamata, Gekkota), and a review of mandibular variation in living species. Mem QLD Mus 41(2):355–366

Hutchinson MN, Mackness BS (2002) Fossil lizards from the Pliocene Chinchilla Local Fauna, Queensland. Rec S Aust Mus 35:169–184

Hutchinson MN, Scanlon JD (2009) New and unusual Plio-Pleistocene Lizard (Reptilia: Scincidae) from Wellington Caves, New South Wales, Australia. J Herpetol 43:139–147

Hutton FW (1874) The geographical relations of the New-Zealand fauna. Ann Mag Nat Hist Ser 4 13(73):25–39

Hutton FW (1875) Notice of the Earnscleugh Cave. Trans Proc N Z Inst 7:138–141

Hutton FW (1899) On the supposed rib of the Kumi, or Ngarara. Trans Proc N Z Inst 31:485

Hutton FW, Drummond J (1904) The animals of New Zealand. An account of the Colony's air-breathing vertebrates. Whitcombe and Tombs, Christchurch

Jones MEH, Tennyson AJD, Worthy JP, Evans SE, Worthy TH (2009) A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*). Proc R Soc B 276:1385–1390. doi:10.1098/rspb.2008.1785

Kamp PJJ, Tripathi ARP, Nelson CS (2014) Paleogeography of Late Eocene to earliest Miocene Te Kuiti Group, central-western North Island, New Zealand. N Z J Geol Geophys 57 (2):128–148

King CM, Roberts CD, Bell BD, Fordyce RE, Nicoll RS, Worthy TH, Paulin CD, Hitchmough RA, Keyes IW, Baker AN, Stewart AL, Hiller N, McDowall BM, Holdaway RN, McPhee RP, Schwarzhans WW, Tennyson AJD, Rust S, McCadie I (2009) Phylum Chordata: lancelets, fishes, amphibians, reptiles, birds, and mammals. In: Gordon DP (ed) New Zealand inventory of biodiversity. Vol 1: Kingdom Animalia. Canterbury University Press, Christchruch, pp 431–527, 566p

Lee MSY, Hutchinson MN, Worthy TH, Archer M, Tennyson AJD, Worthy JP, Scofield RP (2009) Miocene skinks and geckos reveal long-term conservatism of New Zealand's lizard fauna. Biol Lett 5(6):833–837. doi:10.1098/rsbl.2009.0440

Mackness BS, Hutchinson MN (2000) Fossil lizards from the early Pliocene Bluff Downs local fauna. Trans R Soc S Aust 124:17–30

Martin JE, Hutchinson MN, Meredith R, Case JA, Pledge NS (2004) The oldest genus of scincid lizard (Squamata) from the Tertiary Etadunna Formation of South Australia. J Herpetol 38 (2):180–187

Mayr G, Scofield RP (2014) First diagnosable non-sphenisciform bird from the early Paleocene of New Zealand. J R Soc N Z 44:48–56

Mayr G, Scofield RP (2016) New avian remains from the Paleocene of New Zealand: the first early Cenozoic Phaethontiformes (tropic birds) from the Southern Hemisphere. J Vertebr Paleontol 36:e1031343. doi:10.1080/02724634.2015.1031343

Meloro C, Jones MEH (2012) Tooth and cranial disparity in the fossil relatives of *Sphenodon* (Rhynchocephalia) dispute the persistent 'living fossil' label. J Evol Biol 11:2194–2209

Mildenhall DC (1989) Summary of the age and paleoecology of the Miocene Manuherikia Group, Central Otago, New Zealand. J R Soc N Z 19:19–29

Mildenhall DC, Pocknall DT (1989) Miocene-Pleistocene spores and pollen from Central Otago, South Island, New Zealand. N Z Geol Surv Palaeontol Bull 59:1–128

Molnar RE, Wiffen JA (1994) Late Cretaceous polar dinosaur fauna from New Zealand. Cretaceous Res 15:689–706

Morris R, Ballance A (2003) Island magic. Wildlife of the south seas. David Bateman, Auckland

Nielsen SV, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol 59:1–22

Pole M, Douglas BJ (1998) A quantitative palynostratigraphy of the Miocene Manuherikia Group, New Zealand. J R Soc N Z 28:405–420

Pole M, Douglas BJ, Mason G (2003) The terrestrial Miocene biota of southern New Zealand. J R Soc N Z 33:415–426

Pyron RA, Wiens JJ (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. Mol Phylogenet Evol 61:543–583

Reichgelt T, Kennedy EM, Conran JG, Mildenhall DC, Lee DE (2015) The Early Miocene paleolake Manuherikia: vegetation heterogeneity and warm-temperate to subtropical climate in southern New Zealand. J Paleolimnol 53:349–365

Scofield RP, Worthy TH, Tennyson AJD (2010) A heron (Aves: Ardeidae) from the Early Miocene St Bathans Fauna of southern New Zealand. In: Proceedings of the VII international meeting of the Society of Avian Paleontology and Evolution, ed. W.E. Boles and T.H. Worthy. Rec Aust Mus 62(1):89–104

Shea GM (2016) History of discovery of the New Zealand lizard fauna. Chap. 2. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Stevens GR (1980a) New Zealand adrift - the theory of continental drift in a New Zealand setting. A. H. & A. W. Reed, Wellington

Stevens GR (1980b) Southwest Pacific faunal palaeobiogeography in Mesozoic and Cenozoic times: a review. Palaeogeogr Palaeoclimatol Palaeoecol 31:153–196

Stilwell JD, Consoli CP, Sutherland R, Salisbury S, Rich TH, Vickers-Rich PA, Currie PJ, Wilson GJ (2006) Dinosaur sanctuary on the Chatham Islands, Southwest Pacific: first record of theropods from the K–T boundary Takatika Grit. Palaeogeogr Palaeoclimatol Palaeoecol 230:243–250

Strogen DP, Bland KJ, Nicol A, King PR (2014) Paleogeography of the Taranaki Basin region during the latest Eocene–Early Miocene and implications for the 'total drowning' of Zealandia. N Z J Geol Geophys 57(2):110–127

Tennyson AJD, Worthy TH, Jones CM, Scofield RP, Hand SJ (2010) Moa's Ark: Miocene fossils reveal the great antiquity of moa (Aves: Dinornithiformes) in Zealandia. In: Proceedings of the VII international meeting of the society of avian paleontology and evolution, ed. W.E. Boles and T.H. Worthy. Rec Aust Mus 62(1):105–114

Towns DR (1985) The status and prospects of the rare New Zealand lizards *Leiolopisma grande* (Gray), *Cyclodina whitakeri* Hardy and *Leiolopisma otagense* McCann (Lacertilia: Scincidae). In: Grigg G, Shine R, Ehmann H (eds) Biology of Australasian frogs and reptiles. Surrey, Beatty, pp 481–489, 527p

Towns DR, Hitchmough RA, Perrott J (2016) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? Chap. 11. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Whitaker AH (1978) The effects of rodents on reptiles and amphibians. In: Dingwall PR, Atkinson IAE, Hay C (eds) The ecology and control of rodents in New Zealand nature reserves. New Zealand Department of Lands and Survey information series no. 4. New Zealand Department of Lands and Survey, Wellington, pp 75–86

Wiffen J, Molnar RE (1988) First pterosaur from New Zealand. Alcheringa 12:53–59

Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH (2008) Dating the late prehistoric dispersal of polynesians to New Zealand using the commensal Pacific rat. Proc Natl Acad Sci U S A 105:7676–7680

Wilson K-J (2004) Flight of the Huia. Canterbury University Press, Christchurch, 411p

Worthy TH (1987a) Osteological observations of the larger species of skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. N Z J Zool 14:219–229

Worthy TH (1987b) Osteology of *Leiopelma* (Amphibia: Leiopelmatidae) and descriptions of three new subfossil (*Leiopelma*) species. J R Soc N Z 17:201–251

Worthy TH (1991) Fossil skink bones from Northland, New Zealand, including a description of a new *Cyclodina*, Scincidae. J R Soc N Z 21:329–348

Worthy TH (1997) The Quaternary fossil fauna of South Canterbury, South Island, New Zealand. J R Soc N Z 27:67–162

Worthy TH (1998) Quaternary fossil faunas of Otago, South Island, New Zealand. J R Soc N Z 28:421–521

Worthy TH, Holdaway RN (1994) Quaternary fossil faunas from caves in Takaka Valley and on Takaka Hill, northwest Nelson, South Island, New Zealand. J R Soc N Z 24:297–391

Worthy TH, Holdaway RN (1995) Quaternary fossil faunas from caves on Mt Cookson, North Canterbury, South Island, New Zealand. J R Soc N Z 25:333–370

Worthy TH, Holdaway RN (1996) Quaternary fossil faunas, overlapping taphonomies, and palaeofaunal reconstruction in North Canterbury, South Island, New Zealand. J R Soc N Z 26:275–361

Worthy TH, Holdaway RN (2002) The lost world of the moa: prehistoric life of New Zealand. Indiana University Press, Bloomington, IN, Xxxiii + 718p

Worthy TH, Tennyson AJD, Archer M, Musser AM, Hand SJ, Jones C, Douglas BJ, McNamara JA, Beck RMD (2006) Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. Proc Natl Acad Sci U S A 103(51):19419–19423

Worthy TH, Tennyson AJD, Jones C, McNamara JA, Douglas BJ (2007) Miocene waterfowl and other birds from Central Otago, New Zealand. J Syst Palaeontol 5:1–39

Worthy TH, Hand SJ, Nguyen JMT, Tennyson AJD, Worthy JP, Scofield RP, Boles WE, Archer M (2010) Biogeographical and phylogenetic implications of an Early Miocene wren (Aves: Passeriformes: Acanthisittidae) from New Zealand. J Vertebr Paleontol 30:479–498. doi:10.1080/02724631003618033

Worthy TH, Tennyson AJD, Scofield RP (2011a) An Early Miocene diversity of parrots (Aves, Strigopidae, Nestorinae) from New Zealand. J Vertebr Paleontol 31:1102–1116

Worthy TH, Tennyson AJD, Hand SJ, Godthelp H, Scofield RP (2011b) Terrestrial turtle fossils from New Zealand refloat Moa's Ark. Copeia 2011(1):72–76

Worthy TH, Worthy JP, Tennyson AJD, Salisbury SW, Hand SJ, Scofield RP (2013a) Miocene fossils show that kiwi (*Apteryx*, Apterygidae) are probably not phyletic dwarves. In: Göhlich UB, Kroh A (eds) Paleornithological research 2013 – Proceedings of the 8th international meeting of the Society of Avian Paleontology and Evolution. Natural History Museum Vienna, Vienna, p I-XXX + 1–306, pp 63–80. http://verlag.nhm-wien.ac.at/buecher/2013_SAPE_Proceedings/06_Worthy_et_al.pdf. ISBN 978-3-902421-82-1

Worthy TH, Worthy JP, Tennyson AJD, Scofield RP (2013a) A bittern (Aves: Ardeidae) from the Early Miocene of New Zealand. Paleontol J 47(11):1331–1343

Worthy TH, Tennyson AJD, Scofield RP, Hand SJ (2013b) Early Miocene fossil frogs (Anura: Leiopelmatidae) from New Zealand. J R Soc N Z 43(4):211–230

Chapter 4
Putting a Name to Diversity: Taxonomy of the New Zealand Lizard Fauna

Rodney A. Hitchmough, Geoffrey B. Patterson, and David G. Chapple

Abstract The New Zealand lizard fauna is limited to two families, diplodactylid geckos and Eugongylinae skinks. Although its higher-level taxonomic diversity is limited, each family is highly speciose (61 extant skink and 43 extant gecko species). New Zealand lizards are characterised by their ecological, rather than morphological, diversity, which has impeded attempts to delineate and describe species. Numerous species have experienced substantial range reductions following human settlement and the introduction of mammalian predators, whilst others have naturally restricted distributions. Both of these factors have influenced the rate of species discovery and description. However, the implementation of molecular approaches into taxonomic studies has led to an almost threefold increase (38 to 104 extant species) in the number of lizard species recognised. Unfortunately, there remains a large gap between the number of species or taxa recognised in New Zealand and the number that have been formally described (only 55 % of recognised species have been described). Here we provide an overview of the taxonomic history of New Zealand skinks and geckos, outlining the major lineages within each family and providing justification and explanations for the undescribed entities that are recognised. We outline how an integrated morphological and molecular approach can increase the rate of both lizard species discovery and description in New Zealand.

Keywords Gecko • Skink • Taxonomy • Species discovery • Species description • Diplodactylidae • Scincidae

---

R.A. Hitchmough
Department of Conservation, 10-240, Wellington, New Zealand

G.B. Patterson
149 Mairangi Road, Wilton, Wellington, New Zealand

D.G. Chapple (✉)
School of Biological Sciences, Monash University, 25 Rainforest Walk, Clayton, VIC 3800, Australia
e-mail: David.Chapple@monash.edu

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_4

4.1 A Diverse New Zealand Lizard Fauna

New Zealand's lizard fauna combines very low diversity at higher taxonomic levels with extremely high (possibly the highest in the world) species-level diversity for a temperate landmass on a per-area basis (Tables 4.1, 4.2 and 4.3). All of the country's native lizards belong to just two endemic radiations, one of Diplodactylidae geckos and one of Eugongylinae skinks. Both groups have had comprehensive phylogenies published (Chapple et al. 2009; Nielsen et al. 2011) that confirm the monophyly of each.

The lizard fauna of New Zealand is remarkable for its ecological, rather than morphological, diversity. With the notable exception of the diurnal green geckos (genus *Naultinus*), the fauna consists of superficially unremarkable brown, dull green or greyish geckos and skinks. However, both groups are distinguished by pronounced and, in some instances, very extreme K-selection (viviparity of all but one species, low fecundity and great longevity; Cree and Hare 2016). They also use habitats ranging from bare rocks to the canopy and forest floor and from the intertidal zone on the coast to rocky cliffs well above the treeline in mountains where winters are long and snow can fall at any time of the year (Hare et al. 2016).

The taxonomic history of New Zealand's lizards has been strongly influenced by several factors (Shea 2016). Firstly, as a result of mammalian predation (see Towns et al. 2016), lizards were already uncommon on mainland New Zealand when the first European taxonomists and collectors arrived in the country, and they rapidly became even more uncommon due to habitat loss and the introduction of additional mammal species. Collection of specimens was therefore often difficult and serendipitous, and sampling was generally very thin and patchy (Shea 2016). Secondly, many species of both skinks and geckos are superficially very similar to each other, and to confound matters further, there is considerable geographic variation within some species. This made identification of species limits difficult, particularly during the first century of European settlement, when taxonomy tended to be strongly typological in approach. Thirdly, much early work was by visitors to the country or people who never even visited, working on type material deposited by others in Northern Hemisphere museums (Shea 2016). This continued to cause problems well into the twentieth century; for example, McCann (1955), who produced the first comprehensive review of the New Zealand lizard fauna, had no access to the type specimens of many species (S. Bartle pers. comm.), and nomenclatural errors resulted.

The first period of formal taxonomic description of New Zealand's lizards began in the 1830s (Dumeril and Bibron 1836) and continued until the early twentieth century (Boulenger 1906) (Shea 2016). These consisted mostly of descriptions of one or a few species based on one or few specimens, often with very general and limited ('New Zealand' or 'South Sea Islands') and sometimes totally inaccurate, collection locality information. The descriptions were highly variable in quality; some were very brief and did not focus on characters now considered useful to distinguish between closely related species, and some cannot now be associated

Table 4.1 Currently described New Zealand lizard species

Diplodactylidae geckos	Eugongylinae skinks
Dactylocnemis pacificus (Gray, 1842)	*Oligosoma acrinasum* (Hardy, 1977)
Hoplodactylus delcourti Bauer & Russell, 1986 (extinct)	*Oligosoma aeneum* (Girard, 1857)
Hoplodactylus duvaucelii (Duméril & Bibron, 1836)	*Oligosoma alani* (Robb, 1970)
Mokopirirakau cryptozoicus (Jewell & Leschen, 2004)	*Oligosoma burganae* Chapple et al. 2011
Mokopirirakau granulatus (Gray, 1845)	*Oligosoma chloronoton* (Hardy, 1977)
Mokopirirakau kahutarae (Whitaker, 1985)	*Oligosoma fallai* (McCann, 1955)
Mokopirirakau nebulosus (McCann, 1955)	*Oligosoma grande* (Gray, 1845)
Naultinus elegans Gray, 1842	*Oligosoma hardyi* (Chapple, Patterson, Bell & Daugherty, 2008)
Naultinus gemmeus (McCann, 1955)	*Oligosoma homalonotum* (Boulenger, 1906)
Naultinus grayii Bell, 1843	*Oligosoma inconspicuum* (Patterson & Daugherty, 1990)
Naultinus manukanus (McCann, 1955)	*Oligosoma infrapunctatum* (Boulenger, 1887)
Naultinus punctatus Gray, 1842	*Oligosoma judgei* Patterson & Bell, 2009
Naultinus rudis (Fischer, 1882)	*Oligosoma levidensum* (Chapple, Patterson, Bell & Daugherty, 2008)
Naultinus stellatus Hutton, 1872	*Oligosoma lineoocellatum* (Duméril & Duméril, 1851)
Naultinus tuberculatus (McCann, 1955)	*Oligosoma longipes* Patterson, 1997
Toropuku stephensi (Robb, 1980)	*Oligosoma maccanni* (Patterson & Daugherty, 1990)
Tukutuku rakiurae (Thomas, 1981)	*Oligosoma macgregori* (Robb, 1975)
Woodworthia chrysosiretica (Robb, 1980)	*Oligosoma microlepis* (Patterson & Daugherty, 1990)
Woodworthia maculata (Gray, 1845)	*Oligosoma moco* (Duméril & Bibron, 1839)
	Oligosoma nigriplantare (Peters, 1873)
	Oligosoma northlandi (Worthy, 1991) (extinct)
	Oligosoma notosaurus (Patterson & Daugherty, 1990)
	Oligosoma oliveri (McCann, 1955)
	Oligosoma ornatum (Gray, 1843)
	Oligosoma otagense (McCann, 1955)
	Oligosoma pikitanga Bell & Patterson, 2008
	Oligosoma polychroma (Patterson & Daugherty, 1990)
	Oligosoma repens Chapple et al., 2011
	Oligosoma roimata Patterson, Hitchmough & Chapple, 2013
	Oligosoma smithi (Gray, 1845)
	Oligosoma stenotis (Patterson & Daugherty, 1994)

(continued)

Table 4.1 (continued)

Diplodactylidae geckos	Eugongylinae skinks
	Oligosoma striatum (Buller, 1871)
	Oligosoma suteri (Boulenger, 1906)
	Oligosoma taumakae Chapple & Patterson, 2007
	Oligosoma tekakahu Chapple et al., 2011
	Oligosoma toka Chapple et al., 2011
	Oligosoma townsi (Chapple, Patterson, Gleeson, Daugherty, Ritchie, 2008)
	Oligosoma waimatense (McCann, 1955)
	Oligosoma whitakeri (Hardy, 1977)
	Oligosoma zelandicum (Gray, 1843)

The taxonomic authority for each species is provided

with identifiable type specimens. However, sometimes they were extremely thorough and well illustrated, and some type specimens from that era survive in excellent condition (Shea 2016).

There was then almost a 50-year hiatus in species descriptions until the monograph of McCann (1955) summarised knowledge at that time (Shea 2016). McCann, in the absence of access to both the type material and much of the historical literature (S. Bartle pers. comm.), did his best to make sense of the reptile collections in the major New Zealand museums. He synonymised many of the earlier-named species, but also proposed 13 new species and subspecies, four of geckos and nine of skinks. In total he recognised ten endemic gecko species and 20 endemic skink taxa (species and subspecies).

Another, shorter hiatus followed, until a burst of new species descriptions began in the 1970s. Biological exploration of seldom-visited offshore islands and other isolated localities led to the discovery and description of several distinctive new species of both skinks and geckos (Robb 1970, 1975, 1980a; Thomas 1981; Whitaker 1984), and some of McCann's more extreme synonymising (Robb and Rowlands 1977; Robb and Hitchmough 1980) and nomenclatural errors began to be corrected (Gill 1976; Robb 1977; Hardy 1977). Robb (1975) was the first to use genetic data in published herpetological taxonomy in New Zealand.

Hardy (1977) published a taxonomic revision of the New Zealand skink fauna, which included more extensive use of limited genetic data. He described four new species and a subspecies and reinstated the genus *Cyclodina* Girard 1857 for a group of heavy-bodied, nocturnal or crepuscular skinks of humid North Island habitats. Subsequently, researchers at Victoria University of Wellington carried out extensive allozyme electrophoresis surveys of almost the entire known New Zealand lizard fauna (Daugherty et al. 1990; Vos 1988; Hitchmough 1997). This work led to several skink species descriptions (Patterson and Daugherty 1990, 1994; Patterson 1997), recognition of the diurnal New Zealand skinks as an endemic genus (Patterson and Daugherty 1995) and the first insights as to the likely age and monophyly of both the skink and gecko faunas (Daugherty et al. 1994;

Table 4.2 Recognised taxonomically indeterminate (unnamed/undescribed) gecko and skink taxa in New Zealand

Diplodactylidae geckos	Eugongylinae skinks
Dactylocnemis 'Matapia Island'	*Oligosoma* 'Whirinaki' (Barr, Chapple and Hitchmough, unpublished data)
Dactylocnemis 'Mokohinau' (see Chong 1999)	*Oligosoma* aff. *chloronoton* 'West Otago' (Greaves et al. 2007)
Dactylocnemis 'North Cape'	*Oligosoma* aff. *inconspicuum* 'North Otago'*
Dactylocnemis 'Poor Knights' (see Chong 1999)	*Oligosoma* aff. *inconspicuum* 'Okuru'*
Dactylocnemis 'Three Kings'	*Oligosoma* aff. *infrapunctatum* 'Alborn' (Greaves et al. 2008; Patterson & Melzer unpublished morphological data)
Mokopirirakau 'Cascades'	*Oligosoma* aff. *infrapunctatum* 'Chesterfield' (Greaves et al. 2008; Patterson & Melzer unpublished morphological data)
Mokopirirakau 'Cupola'*	*Oligosoma* aff. *infrapunctatum* 'cobble' (Greaves et al. 2008; Patterson & Melzer unpublished morphological data)
Mokopirirakau 'Okarito'	*Oligosoma* aff. *infrapunctatum* 'crenulate' (Greaves et al. 2008)
Mokopirirakau 'Open Bay Islands'	*Oligosoma* aff. *infrapunctatum* 'Hokitika' (Greaves et al. 2008; Patterson & Melzer unpublished morphological data)
Mokopirirakau 'Roys Peak'	*Oligosoma* aff. *infrapunctatum* 'Southern North Island' (Greaves et al. 2008)
Mokopirirakau 'southern forest'	*Oligosoma* aff. *infrapunctatum* 'Westport' (Greaves et al. 2008)
Mokopirirakau 'southern North Island'	*Oligosoma* aff. *lineoocellatum* 'Central Canterbury' (Greaves et al. 2007)
Naultinus 'North Cape'	*Oligosoma* aff. *lineoocellatum* 'Mackenzie Basin' (Greaves et al. 2007)
Toropuku 'Coromandel'	*Oligosoma* aff. *lineoocellatum* 'South Marlborough' (Greaves et al. 2007)
Woodworthia 'Central Otago'	*Oligosoma* aff. *longipes* 'Rangitata' (Chapple et al. 2009)
Woodworthia 'Cromwell'	*Oligosoma* aff. *longipes* 'southern' (Chapple et al. 2009)
Woodworthia 'Kaikouras'*	*Oligosoma* aff. *polychroma* Clade 2 (Liggins et al. 2008)
Woodworthia 'Marlborough mini'	*Oligosoma* aff. *polychroma* Clade 3 (Liggins et al. 2008)
Woodworthia 'Mount Arthur'	*Oligosoma* aff. *polychroma* Clade 4 (Liggins et al. 2008)
Woodworthia 'Otago/Southland large' (may be further subdivided into four entities)	*Oligosoma* aff. *polychroma* Clade 5 (Liggins et al. 2008)
Woodworthia 'pygmy'	*Oligosoma* aff. *smithi* 'Three Kings, Te Paki, Western Northland' (Hare et al. 2008)

(continued)

Table 4.2 (continued)

Diplodactylidae geckos	Eugongylinae skinks
Woodworthia 'Southern Alps'	*Oligosoma* sp. 'Homer Tunnel' (Chapple, Jewell and Hitchmough, unpublished data)
Woodworthia 'southern mini'	
Woodworthia aff. *maculata* 'Muriwai' (Hitchmough, van Winkel and Nielsen, unpublished data)	
Woodworthia cf. *brunnea*	

For geckos, most have published phylogenetic support in Nielsen et al. (2011). Exceptions in the genus *Dactylocnemis* were identified in the BSc honours project of Chong (1999). One other recent discovery is supported by unpublished genetic data (Hitchmough, van Winkel and Neilsen, unpublished data), and other exceptions with absent or contradictory genetic information are labelled with an asterisk. For skinks, most have phylogenetic support in Chapple et al. (2009) or other molecular studies (listed below). Exceptions that lack relevant genetic information are labelled with an asterisk.

Table 4.3 Increase in described and recognised New Zealand lizard species/taxa since McCann (1955)

Assessment year	Publication	Geckos	Skinks	Total
1955	McCann (1955)	10	20	30
1980	Newman (1982)	16 + 1 = 17	21	37 + 1 = 38
1994	Daugherty et al. (1994)	16 + 13 = 29	27 + 4 = 31	43 + 17 = 60
2001	Hitchmough (2002)	17 + 25 = 42	28 + 9 = 37	45 + 34 = 79
2005	Hitchmough et al. (2007)	18 + 25 = 43	28 + 16 = 44	46 + 41 = 87
2009	Hitchmough et al. (2010)	18 + 24 = 42	34 + 21 = 55	52 + 45 = 97
2012	Hitchmough et al. (2013)	18 + 24 = 42	38 + 17 = 55	56 + 41 = 97
2015	Hitchmough et al. (2016)	19 + 25 = 44	40 + 22 = 62	59 + 47 = 106

Additional lizard species estimates were produced in 1980 (Newman 1982) and 1994 (Daugherty et al. 1994) and through sequential New Zealand Threat Classification System conservation status assessments in 2001 (Hitchmough 2002), 2005 (Hitchmough et al. 2007), 2009 (Hitchmough et al. 2010), 2012 (Hitchmough et al. 2013) and 2015 (Hitchmough et al. 2016). Figures in each cell refer to taxa that are taxonomically determinate (formally named) and taxonomically indeterminate (unnamed/undescribed).

Chambers et al. 2001). It also facilitated the development of a very comprehensive frozen tissue collection for both groups. This has subsequently been used for DNA sequencing, which has led to robust phylogenies (Chapple et al. 2009; Nielsen et al. 2011).

This genetic work over the last three decades has led to the identification of a very large number of cryptic species in both groups, more than trebling the size of the known fauna (Tables 4.1, 4.2 and 4.3). Many of these species remain formally unnamed, although work on descriptions is in progress (Hitchmough, unpublished data; Chapple, Patterson and Melzer, unpublished data). Once the taxonomic unit has been delineated by genetic techniques, morphological examination, in almost every case, allows the identification of diagnostic physical characters, although

Table 4.4 Details (identities, discovery dates, taxonomic authors [for subsequently described species] and supporting references) of the novel taxa discovered, since McCann's (1955) monograph that were immediately suspected to be new species

Species and authority or reference	Discovery date
Woodworthia chrysosiretica (Robb 1980)	1960s
Mokopirirakau 'Cupola' (see Newman 1982)	1968
Tukutuku rakiurae (Thomas 1981)	1969
Mokopirirakau kahutarae (Whitaker 1984)	1970
Mokopirirakau 'Open Bay Islands' (see Newman 1982)	1970
Mokopirirakau 'cascades' (see Newman 1982)	1974
Oligosoma inconspicuum (Patterson & Daugherty 1990—later identified as *O. burganae* (Chapple et al. 2011))	1981
Oligosoma longipes Patterson 1997	1983
Oligosoma microlepis (Patterson and Daugherty 1990)	1985
Dactylocnemis 'Matapia' (see Pickard and Towns 1988—misidentified as *W. chrysosiretica*)	1986
Oligosoma taumakae (Chapple and Patterson, 2007)	1988
Oligosoma aff. *infrapunctatum* 'Chesterfield' (see Aviss and Lyall 1995)	1993
Oligosoma aff. *infrapunctatum* 'Alborn' (see Lettink and Stengs 2014)	1993
Mokopirirakau cryptozoicus (Jewell and Leschen, 2004)	1996
Mokopirirakau 'Roys Peak' (see Tocher and Marshall 2001)	1998
Oligosoma aff. *inconspicuum* 'Okuru' (Department of Conservation BioWeb Herpetofauna database)	2000
Oligosoma tekakahu Chapple et al. 2011 (M. Tocher pers. comm. to R. Hitchmough; Loh 2003)	2002
Oligosoma 'Whirinaki' (the late A.H. Whitaker pers. comm. to R. Hitchmough)	2003
Oligosoma aff. *longipes* 'Rangitata' (Department of Conservation BioWeb Herpetofauna database)	2004
Oligosoma pikitanga Bell and Patterson 2008	2004
Oligosoma judgei Patterson and Bell 2009	2005
Oligosoma repens Chapple et al. 2011 (T. Jewell pers. comm. to R. Hitchmough)	2005
Oligosoma aff. *infrapunctatum* 'cobble' (Jewell 2008)	2006
Oligosoma aff. *inconspicuum* 'North Otago' (T. Jewell pers. comm. to R. Hitchmough; flickr)	2008
Woodworthia aff. *maculata* 'Muriwai' (D. van Winkel pers. comm. to R. Hitchmough)	2010
Oligosoma sp. 'Homer Tunnel' (T. Jewell pers. comm. to R. Hitchmough)	2014

substantial geographic variation in body size, colour and morphology within some genetic clades can be confusing.

In addition to the identification of distinct taxa using genetic analysis of already known populations, completely new discoveries of totally novel species continue (T. Jewell, pers. comm.). Novel discoveries which were immediately suspected to be new species, found since publication of the monograph of McCann (1955), are listed in Table 4.4. All but three of these discoveries (*Oligosoma* 'Okuru', *Oligosoma* aff. *inconspicuum* 'North Otago' and *Mokopirirakau* 'Cupola') are now supported as distinct taxa by genetic data. This discovery curve shows no sign of flattening out (Table 4.3), and further discoveries are highly likely.

The regularly revised conservation status lists, generated using the New Zealand Threat Classification System (Townsend et al. 2008), provide a regular update of the size of the known fauna. This system has a precautionary approach and includes taxonomically indeterminate (undescribed) species with a wide range of degree of evidential support for their distinctiveness. Some of these entities are recent discoveries that may not survive the process of formal scientific examination and peer-reviewed publication of a description. However, all have been accepted by a panel of experts as having a reasonable level of evidence for their possible taxonomic distinctiveness, and the majority already have strong genetic support for their separate species status. The number of taxa included in these lists has increased steadily from 2001 to the present (Table 4.3).

4.2 Taxonomic History of New Zealand Skinks (Scincidae, Eugongylinae)

4.2.1 Higher-Level Relationships

Globally, there are seven subfamilies of skinks: Acontinae, Egerniinae, Eugongylinae, Lygosominae, Mabuyinae, Sphenomorphinae and Scincinae (Uetz and Hosek 2015). The Eugongylinae is monophyletic and is distributed throughout Australia, Papua New Guinea, the southwest Pacific (including New Zealand), southeast Asia and Africa (Smith et al. 2007; Skinner et al. 2011; Brandley et al. 2015). All native New Zealand skink species are endemic and members of Eugongylinae (Smith et al. 2007; Chapple et al. 2009). The closest relative of the New Zealand skink radiation is *Oligosoma lichenigerum*, which occurs on Lord Howe Island and Norfolk Island (Smith et al. 2007; Chapple et al. 2009). The sister lineage of New Zealand *Oligosoma* + *O. lichenigerum* is *Lioscincus* from New Caledonia, which suggests that skinks colonised New Zealand from New Caledonia via long-distance overwater dispersal and island-hopping along the Lord Howe Rise and Norfolk Ridge (Smith et al. 2007; Chapple et al. 2009; Chapple and Hitchmough 2016; D.G. Chapple, unpublished data).

4.2.2 Generic Relationships

Prior to the first modern taxonomic revision of New Zealand skinks by McCann (1955), there was substantial instability in the generic assignment of species (Shea 2016). Species were variously placed in *Mocoa*, *Lygosoma*, *Tiliqua*, *Cyclodina* and several other genera (*Oligosoma*, *Hinulia*, *Euprepes*, *Lygosomella*, *Norbea*, *Hombronia*; see Hardy 1977; Chapple et al. 2009). However, McCann (1955) placed 17 of the 18 species known at the time in *Leiolopisma*, with the remaining species placed in *Sphenomorphus* (*S. pseudornatus*). Hardy (1977) subsequently resurrected *Cyclodina* Girard to accommodate *C. alani*, *C. macgregori*, *C. oliveri*, *C. whitakeri*, *C. aenea* and *C. ornata* (the latter two species were previously part of *S. pseudornatus*). Two decades later, Patterson and Daugherty (1995) retained *Cyclodina*, but reinstated *Oligosoma* Girard to accommodate all New Zealand *Leiolopisma* species.

Although morphological and ecological differences were evident between *Oligosoma* (shallow pointed heads, long limbs and toes and bodies that are oval in cross section; generally diurnal species that prefer open habitats where they are overt baskers) and *Cyclodina* (deeper and blunter heads, relatively shorter limbs and toes and bodies that are squarish in cross section; nocturnal or crepuscular species that prefer more shaded habitats) (Patterson and Daugherty 1995; Gill and Whitaker 2001), Chapple et al. (2009) demonstrated that each was not reciprocally monophyletic. Instead, the '*Cyclodina*' and '*Oligosoma*' body plans each appear to have evolved on multiple occasions. Whilst eight major genetic clades have been identified within New Zealand skinks, Chapple et al. (2009) were unable to diagnose each on the basis of morphological characters due to the morphological conservatism present, presumably caused by the rapid radiation of skinks following their arrival in New Zealand. Thus, in order to ensure taxonomic stability, Chapple et al. (2009) elected to assign all native New Zealand skink species to a single genus, *Oligosoma*.

The phylogenetic relationships among the eight main clades of New Zealand skinks were poorly resolved (Chapple et al. 2009). The only well-supported relationships were among Clades 1 (*O. longipes* complex, *O. polychroma* complex, *O. lineoocellatum-chloronoton* complex, *O. maccanni*, *O. notosaurus-inconspicuum* complex, *O. grande*, *O. stenotis*) and 2 (*pikitanga*, *judgei*, *otagense*, *waimatense*, *taumakae*, *acrinasum*, *infrapunctatum* complex) (Chapple et al. 2009).

4.2.3 Species Recognition

Of the eight major genetic clades within *Oligosoma* skinks (Chapple et al. 2009), Clade 1 is the most widespread, with species within this clade distributed across the southern North Island, South Island and Stewart Island. It is also the most speciose clade (14 described species, 12 undescribed taxa; Tables 4.1 and 4.2), comprising members of the *O. longipes* species complex (*O. longipes*, *O.* aff. *longipes* 'Rangitata', *O.* aff. *longipes* 'southern'; Chapple et al. 2009), *O. nigriplantare*, members of the *O. polychroma* species complex (*O. polychroma*, *O.* aff. *polychroma* Clade 2, *O.* aff. *polychroma* Clade 3, *O.* aff. *polychroma* Clade 4, *O.* aff. *polychroma* Clade 5; Liggins et al. 2008), members of the *O. chloronoton-lineoocellatum* species complex (*O. chloronoton*, *O.* aff. *chloronoton* 'West Otago', *O. lineoocellatum*, *O.* aff. *lineoocellatum* ‘Central Canterbury’, *O.* aff. *lineoocellatum* ‘Mackenzie Basin’, *O.* aff. *lineoocellatum* ‘South Marlborough’; Greaves et al. 2007), *O. maccanni*, members of the *O. inconspicuum–O. notosaurus* species complex (*O. burganae*, *O. inconspicuum*, *O.* aff. *inconspicuum* ‘North Otago’, *O.* aff. *inconspicuum* ‘Okuru’, *O. notosaurus*, *O. repens*, *O. tekakahu*, *O. toka*; Chapple et al. 2011), *O. grande* and *O. stenotis*. The undescribed taxonomic diversity in the *O. polychroma* (Liggins et al. 2008) and *O. chloronoton-lineoocellatum* complexes (Greaves et al. 2007) is due to molecular studies identifying deep genetic splits within these widespread species (though a recent morphological study suggests the presence of an additional taxon within *O. lineoocellatum*; Patterson and Melzer, unpublished data). In contrast, the taxonomic diversity within the *O. inconspicuum-notosaurus* complex is the result of the discovery of several morphologically distinct taxa in remote regions of the South Island, as well as molecular studies identifying deep genetic splits within *O. inconspicuum* (Chapple et al. 2011). The undescribed taxa within the *O. longipes* complex reflect both genetic substructure within *O. longipes* (*O.* aff. *longipes* ‘southern’; Chapple et al. 2009) and the discovery of a morphologically distinct, sympatric population (*O.* aff. *longipes* ‘Rangitata’; Tables 4.2 and 4.4).

Clade 2 is predominately a South Island radiation (all apart from two members of the *O. infrapunctatum* complex). It includes seven described species and eight undescribed taxa: *O. pikitanga*, *O. judgei*, *O.* sp. ‘Homer Tunnel’, *O. otagense*, *O. waimatense*, *O. taumakae*, *O. acrinasum* and members of the *O. infrapunctatum* species complex (*O. infrapunctatum*, *O.* aff. *infrapunctatum* ‘Alborn’, *O.* aff. *infrapunctatum* ‘Chesterfield’, *O.* aff. *infrapunctatum* ‘cobble’, *O.* aff. *infrapunctatum* ‘crenulate’, *O.* aff. *infrapunctatum* ‘Hokitika’, *O.* aff. *infrapunctatum* ‘Southern North Island’, *O.* aff. *infrapunctatum* ‘Westport’; Greaves et al. 2008; Hitchmough et al. 2016; Tables 4.1 and 4.2). The undescribed species diversity within the *O. infrapunctatum* species group is concentrated (for all but ‘Southern North Island’ and *O.* aff. *infrapunctatum* ‘crenulate’) along the northwest coast of the South Island (Westland), with the putative species having restricted, isolated distributions (Chapple and Hitchmough 2016; Table 4.2). A recent morphological study indicates that an additional *O. infrapunctatum* taxon may exist in the Heaphy Track region (Patterson and Melzer, unpublished data).

Clade 3 contains three species that were formally part of *Cyclodina*: *O. aeneum*, *O. hardyi* and *O. levidensum*. *Oligosoma aeneum* is widely distributed throughout the North Island (and several offshore islands), whilst *O. hardyi* is restricted to the Poor Knights Islands and *O. levidensum*, the smallest native New Zealand skink species, to the Te Paki region at the northern tip of Northland (Chapple and Hitchmough 2016). A detailed taxonomic revision of the former *C. aenea* species complex was completed recently (Chapple et al. 2008a), and therefore there are unlikely to be any additional species present within this clade.

Clade 4 comprises the majority of the species previously assigned to *Cyclodina* (*O. ornatum*, *O. roimata*, *O. townsi*, *O. oliveri, O. whitakeri*, *O. macgregori*, *O. alani*), along with the Three Kings Islands skink (*O. fallai*). All species occur in the North Island, with several endemic to offshore islands (*O. roimata*, *O. townsi*, *O. oliveri*, *O. fallai*). Given the recent taxonomic activity within this clade (Chapple et al. 2008b; Patterson et al. 2013), no additional species are expected.

Clade 5 contains three forest-dwelling species with arboreal tendencies (*O. zelandicum*, *O. striatum* and *O. homalonotum*; Neilson 2002; Neilson et al. 2004) and the recently discovered 'Whirinaki' skink, which appears to be a sister species to *O. zelandicum*. The distribution of *O. zelandicum* ranges from the Taranaki region in the North Island, across Cook Strait to the Westland region of the South Island (O'Neill et al. 2008). In contrast, *O. striatum* occurs in the central-northern North Island, whilst *O. homalonotum* is restricted to Great Barrier and Little Barrier Islands. The synonymy of *O. gracilicorpus* with *O. homalonotum* (Chapple et al. 2009) suggests that *O. homalonotum* was also formerly found on the Northland mainland. The 'Whirinaki' skink is known (from video footage) from the Whirinaki forest in the central North Island and (from specimens) from Bream Head near Whangarei (B. Barr, D.G. Chapple, R.A. Hitchmough, unpublished data; Tables 4.2 and 4.4).

The egg-laying skink, *O. suteri*, is the sole member of Clade 6. *Oligosoma suteri* is restricted mainly to islands off the coast of the northeastern North Island and exhibits extremely low levels of intraspecific genetic divergence across its range (Hare et al. 2008).

Oligosoma moco is the only member of Clade 7 (Chapple et al. 2009). It occurs on the east coast of the North Island, northwards from the Bay of Plenty and throughout the islands off the northeastern coast of the North Island. A recent molecular study showed substantial genetic structuring within *O. moco*, with a mean pairwise genetic distance (GD) of 2.7 % and three clades identified, but this was interpreted as intraspecific geographic population structuring (Hare et al. 2008). The northernmost and southernmost populations were not included in this study.

The final clade, Clade 8, contains members of the *O. smithi-microlepis* species complex (*O. microlepis*, *O. smithi*, *O.* aff. *smithi* 'Three Kings, Te Paki, Western Northland'). *O. smithi* occurs on beaches and islands along the northeast of the North Island, whilst *O.* aff. *smithi* 'Three Kings, Te Paki, Western Northland' occurs on the Three Kings Islands and along the west coast of Northland (Hare et al. 2008). *O. microlepis* has a patchy distribution in the central North Island (Hare et al. 2008). Morphological investigations remain to be conducted to ascertain whether the three taxa within the species complex represent distinct species.

In total, therefore, there are 39 named extant (and 1 extinct) species of New Zealand skinks and 22 taxonomically indeterminate entities.

4.3 Taxonomic History of New Zealand Geckos (Diplodactylidae)

4.3.1 Higher-Level Relationships

The history of family-level taxonomy of the group including the New Zealand geckos was extremely confused, until resolved by Han et al. (2004). The

New Zealand geckos are now considered to belong to the family Diplodactylidae, along with three other distinct groups: the New Caledonian gecko radiation (genera *Bavayia*, *Correlophus*, *Dierogekko*, *Eurydactylodes*, *Mniarogekko*, *Oedodera*, *Paniegekko*, *Rhacodactylus*) and two distinct clades in Australia, *Pseudothecadactylus* which is a sister clade to the New Caledonian radiation and a larger clade (*Amalosia*, *Crenadactylus*, *Diplodactylus*, *Hesperoedura*, *Lucasium*, *Nebulifera*, *Oedura*, *Rhynchoedura*, *Strophurus*) which is a sister clade to the New Zealand clade (Nielsen et al. 2011). The Diplodactylidae are part of an Australasian radiation of three gekkotan families and are the sister group of the Carphodactylidae plus the legless Pygopodidae (Han et al. 2004; Nielsen et al. 2011).

4.3.2 Generic Relationships

Within New Zealand, McCann (1955), in the first modern taxonomic review of the New Zealand lizard fauna, recognised ten endemic gecko species divided into three genera: *Hoplodactylus* Fitzinger 1843 ('brown geckos'), *Naultinus* Gray 1842 (North Island 'green geckos') and *Heteropholis* Fischer 1882 (South Island 'green geckos'). *Heteropholis* was subsequently synonymised with *Naultinus* (Bauer 1990), and a diversity of new species, chiefly *Hoplodactylus*, was described, resulting in 20 currently recognised, named species (Daugherty et al. 1994; Jewell and Leschen 2004). However, cryptic diversity revealed by allozyme (Daugherty et al. 1994; Hitchmough 1997) and preliminary mitochondrial DNA sequence data (Chambers et al. 2001) suggested that many additional, unnamed taxa exist.

Bauer (1990) regarded *Naultinus* as monophyletic and a sister to remaining members of the clade, but intra-generic relationships could not be resolved. *Hoplodactylus* was paraphyletic with respect to the New Caledonian forms, but was also poorly resolved. Based on allozyme data, Hitchmough (1997) concluded that New Zealand geckos were monophyletic and sister to the New Caledonian clade. He recognised three complexes within *Hoplodactylus*: the *Hoplodactylus maculatus* complex, the *Hoplodactylus pacificus* complex and the *Hoplodactylus granulatus* complex. These complexes, as well as *Naultinus*, corresponded to two general, morphological groupings: a broad-toed clade, including only the *H. maculatus* group; and a narrow-toed clade, comprising remaining *Hoplodactylus* plus *Naultinus*. Although some nodes received high support, on the whole, relationships within the different groups were poorly resolved and/or weakly supported. Hitchmough (1997) considered this poor support to be a result of short branch lengths, which could signify a rapid radiation of these species.

A subsequent analysis of 16S mtDNA, conducted by Chambers et al. (2001), found New Zealand and New Caledonian diplodactylids to be reciprocally monophyletic and largely supported Hitchmough's (1997) within-group relationships. Chambers et al. (2001) recognised the necessity to erect at least two new genera to maintain the monophyly of *Hoplodactylus* whilst preserving the name, *Naultinus*, for the distinctive and long-recognised green geckos, but they did not complete a generic revision themselves.

Nielsen et al. (2011) used both mitochondrial and nuclear DNA sequences to answer many long-standing questions about the evolution and systematics of New Zealand's geckos. Seven genera are now recognised as a result of their work: *Dactylocnemis*, *Hoplodactylus*, *Mokopirirakau*, *Naultinus*, *Toropuku*, *Tukutuku* and *Woodworthia*. *Hoplodactylus*, which formerly included all the New Zealand geckos, except the diurnal, brightly coloured *Naultinus*, was rendered paraphyletic by the confirmation that *Naultinus*, rather than being the sister group to the remainder of the New Zealand radiation (as had been thought prior to the work of Chambers et al. 2001), was nested deep within the radiation. To retain generic monophyly, either the highly distinctive *Naultinus* would have to have been included in *Hoplodactylus*, or splitting of *Hoplodactylus* was required. Unlike the New Zealand skinks, which show a very bushy pattern of evolution, with many branching events in very quick succession near the base of the clade, the geckos show strong structure with seven clear groups separated by long branches. The decision was therefore made by Nielsen et al. (2011) to name each of these groups as a genus. Each is also readily diagnosable by morphology (again unlike most possible subgroups of skinks).

Within the New Zealand radiation, there was an initial split between a group with broadly expanded toe pads, v-shaped or strongly curved distal lamellae and flesh-coloured, unpigmented mouth lining (*Hoplodactylus* and *Woodworthia*) and the remaining genera, three of which (*Mokopirirakau*, *Naultinus* and *Tukutuku*) have narrow toes, straight to only slightly curved lamellae and intense yellow and/or blue to black pigment in the mouth. *Dactylocnemis* and *Toropuku* are morphologically anomalous. In particular, *Dactylocnemis* most closely matches *Hoplodactylus* and *Woodworthia* in external morphology, to the extent that all *Dactylocnemis*, *Toropuku* and *Woodworthia* were considered to be a single variable species (*Hoplodactylus pacificus*) between 1955 (McCann 1955) and 1977 (Robb and Rowlands 1977). *Toropuku* is closer to *Mokopirirakau*, *Naultinus* and *Tukutuku* in some aspects of morphology, but appears morphologically intermediate between them and *Dactylocnemis*. *Toropuku* was briefly considered conspecific with *Dactylocnemis* to the exclusion of *Woodworthia* under the name *Hoplodactylus pacificus* by Robb and Rowlands (1977), but this was quickly reversed by the naming of *T. stephensi* (as *Hoplodactylus stephensi*) by Robb (1980a). Morphology therefore strongly suggests *Dactylocnemis*, and then *Toropuku*, to be the most basal members of the narrow-toed clade, but they are nested among the other narrow-toed genera in the DNA-based phylogeny of Nielsen et al. (2011). However, the meta-analysis of Pyron et al. (2013) placed *Dactylocnemis* and *Toropuku* as the sister group to *Mokopirirakau*, *Naultinus* and *Tukutuku*.

The narrow-toed genera, *Mokopirirakau*, *Naultinus* and *Tukutuku*, are strongly arboreal (particularly the first two), avid baskers (R. Hitchmough, pers. obs.) and often confine their use of retreats to periods of adverse weather, relying on camouflage whilst inactive at other times (Romijn et al. 2013; Hare et al. 2007; L. Moran, New Zealand Department of Conservation, pers. comm. to R. Hitchmough).

Naultinus is diurnal (Hare et al. 2007), and the other two can be active both by day and by night (Romijn et al. 2013; L. Moran, New Zealand Department of Conservation, pers. comm. to R. Hitchmough). The other genera are more strictly nocturnal (although they will emerge to bask near their retreats). They consistently use daytime retreats (Gibson et al. 2015) and are generally considered more terrestrial, though all forage, generally use crevice retreats on the ground, but also use crevice retreats in shrubs and trees if these occur in their habitat (Jewell and McFarlane 1997; Hoare et al. 2007, Barry et al. 2014).

4.3.3 Species Recognition

The genus *Tukutuku,* erected by Nielsen et al. (2011), contains only a single species, *T. rakiurae* (Thomas 1981). This species has a restricted distribution in southern Stewart Island, so barring new discoveries elsewhere, this is unlikely to change (Tables 4.1 and 4.2).

Toropuku, another genus erected by Nielsen et al. (2011), has a single described species, *T. stephensi* (Robb 1980a), which is found on two islands in Cook Strait (Table 4.1). However, in 1997, not long after the second of these Cook Strait populations was found (in 1990; Whitaker 1991), specimens of *Toropuku* began to be discovered at Coromandel, 500 km to the north (Whitaker et al. 1999; Table 4.2). They have now been found over a large part of the Coromandel Peninsula, although never by deliberate searching, and only in small numbers at each site. Preliminary investigations suggested that these populations were genetically distinct from but conspecific with *T. stephensi*. However, after comparing genetic and morphological divergence of the two regional populations, with the divergence between species within *Naultinus* and *Mokopirirakau* (the sister clades to *Toropuku*; Nielsen et al. 2011; Hitchmough et al. unpublished data), both are now considered to be distinct species. A description is in preparation.

In contrast to all other New Zealand lizard genera, and reflecting its strikingly bright and often polymorphic colours and colour patterns, *Naultinus* Gray 1842 has historically been over-split (Tables 4.1 and 4.2). This includes a history of synonymies of names based on colour morphs, and including generic synonymy; the generic name *Heteropholis* Fischer, 1882 was used for the South Island species between 1955 (McCann 1955) and 1990 (Bauer 1990). Most recently *N. poecilochlorus* (Robb 1980a, b) has been synonymised with *N. tuberculatus* by Neilsen et al. (2011). Only one undescribed species was identified by Nielsen et al. (2011). Currently recognised species are *N. gemmeus* (McCann, 1955); *N. tuberculatus* (McCann, 1955); *N. stellatus* Hutton, 1872; *N. rudis* (Fischer, 1882); *N. manukanus* (McCann, 1955); *N. punctatus* Gray, 1842; *N. elegans* Gray, 1842, and *N. grayii* Bell, 1843. An additional species from the Te Paki area is morphologically and genetically distinct, and a description is in preparation.

Mokopirirakau was erected by Nielsen et al. (2011) for forest and alpine geckos (Tables 4.1 and 4.2). The forest gecko, *M. granulatus* (Gray, 1845), is one of the longer-recognised species in the fauna and was previously regarded as occurring in forests and shrublands throughout most of the country, except the lower-rainfall eastern parts of the South Island and the northern part of Northland. However, McCann (1955) separated the Stewart Island population as *M. nebulosus* (McCann, 1955) (although he originally placed it incorrectly in *Heteropholis*, which is now part of *Naultinus*). *Mokopirirakau kahutarae* (Whitaker 1984), the first alpine member of the genus to be discovered, was found accidentally by an ornithological expedition in the Kaikoura Ranges in 1970. *Mokopirirakau cryptozoicus* (Jewell and Leschen 2004) was discovered in somewhat similar, high-altitude rocky habitat in the Takitimu Range in 1996, and an additional two alpine species, one from northern Fiordland and the other from western Otago, have had their distinctiveness confirmed by genetic (Nielsen et al. 2011) and morphological analysis, and descriptions are in preparation (Hitchmough, Neilsen, Bauer, unpublished data). Another possible alpine species from the Nelson Lakes area is far more poorly known, and its genetics have not yet been examined. In addition, two new lowland species from south Westland, one species from the southern North Island and one species from the Catlins and Southland, await splitting from *M. granulatus* following confirmation of their genetic and morphological distinctiveness (Nielsen et al. 2011). This makes a total of four named species, six with descriptions in preparation and one more awaiting further work to confirm its distinctiveness.

Dactylocnemis was erected as a new genus by Fitzinger (1861) for his *Dactylocnemis wüllerstorfii* (now regarded as a nomen nudum). Steindachner (1869) used this generic name for *D. pacificus*, making it available when the former *Hoplodactylus pacificus* complex was elevated to genus level by Nielsen et al. (2011). The phylogenetics of this group was investigated by Chong (1999), and her work, together with additional information from Nielsen et al. (2011), provides very strong evidence that *D. pacificus* should be split into six deeply divergent, congeneric species (Tables 4.1 and 4.2). Three of these species are endemics of single island groups (the Three Kings, Poor Knights and Mokohinaus/Pokohinaus), and two occur in sympatry in Te Paki and on surrounding small islands, with the distribution of one of these species also extending to the Karikari Peninsula. *D. pacificus* itself occupies the balance of that species' range as formerly understood (Robb and Rowlands 1977; Robb 1980a, b). However, the identity of populations between the Bay of Islands and Kaitaia requires confirmation.

Hoplodactylus Fitzinger 1843 now contains only a single extant species, the large *H. duvaucelii* (Dumeril and Bibron 1836) (Tables 4.1 and 4.2). The genus also contains the giant, extinct *H. delcourti* Bauer and Russell, 1986, which, anomalously is known only from a single stuffed museum specimen with no locality data; strangely there are no known fossil remains of this species (see Shea 2016; Worthy 2016). *H. duvaucelii* contains two quite distinct groups of extant populations; one population occurs on islands in Cook Strait, and the other occurs off the northeastern North Island. These form distinct, reciprocally monophyletic genetic subclades, which differ in body size, scalation and colour pattern, and may thus potentially have been regarded as distinct species. However, the current distribution is a result of range contractions due to extinction elsewhere as a result of predation by invasive mammals; bones of *H. duvaucelii* have been found in caves and pre-European-era predator middens across most of both major islands of New Zealand (Worthy 1987; Worthy and Holdaway 2002, Worthy 2016). In 2010, decades after the most recent mainland record, a survivor was accidentally collected in a mainland sanctuary in the Waikato region (Morgan-Richards et al. 2016). Genetic and morphological analysis of this specimen showed that it had a mix of genetic alleles and morphological characters otherwise confined to the northern or Cook Strait subclades (Morgan-Richards et al. 2016). This was interpreted as evidence that these subclades are conspecific and were previously connected by mainland gene flow.

The final genus, *Woodworthia* Garman, 1901, contains two described species, *W. maculata* (Gray, 1845) and *W. chrysosiretica* (Robb 1980a, b) (Tables 4.1 and 4.2). The generic name is feminine, so the endings of the specific names changed from—*us* to—*a* to match it in gender. *Woodworthia* also has nine new species with descriptions in preparation (although one of these probably has an available existing name, *W. brunnea* (Cope 1869)). In addition, one of these nine species (*W.* 'Otago/Southland large') has four very distinct subgroups, which might each warrant separate description. The inclusion of an additional taxon in *Woodworthia* (*W.* 'Kaikouras') was very strongly supported by the allozyme study of Hitchmough (1997). This taxon is readily distinguishable by morphology, but it was not recovered as a distinct mitochondrial DNA clade by Nielsen et al. (2011); instead each population clustered closely with the adjacent or sympatric population of *W.* 'Marlborough mini'. This probably indicates a hybrid origin, but as the two sampled populations are quite widely separated geographically but share allozyme and morphological characters, indicating evolutionary cohesiveness, it may still justify formal description as a species. A very recent discovery (2010) was a population of *Woodworthia* on the Auckland west coast (Muriwai). This is the close genetic sister group to *W. maculata* sensu stricto, but has much shorter distal phalanges and a distinctive colour pattern (D. van Winkel pers. comm.); this may represent another undescribed species. *Woodworthia* therefore has two named species, nine with descriptions in preparation and up to five additional candidates for species status.

In total, therefore, there are 18 named extant (and one extinct) species of New Zealand gecko; 22 well-known, unnamed species with descriptions in preparation; and up to six additional possible new species (Tables 4.1 and 4.2).

4.4 Enhancing the Rate of Species Discovery and Description

To identify new species, it is necessary to have a clear definition of what constitutes a species (Coyne and Orr 2003). At a single place and time, it will be obvious that some groups of organisms exchange genes by breeding with each other and are therefore obviously the same species, whereas others never do so and are therefore clearly different species. However, when the same organisms are examined across a broad landscape or over geological time frames, that simple dichotomy becomes blurred; species vary in size and appearance across the landscape; some pairs of related species never interbreed, even when they are in contact; some produce rare, non-viable or sterile hybrids; some meet at narrow hybrid zones where frequent hybridisation, but little gene flow, occurs between the parental species; and others occur in broader zones where the species or populations merge. Other pairs of closely related populations are never found in contact with each other, so natural reproductive isolation cannot be used to assess species status. To define species, we use an evolutionary species concept (Wiley 1981), where either evidence of reproductive isolation or, if they are not in contact, of long-term independent evolutionary trajectories indicates separate species status. Evidence for independent trajectories includes very deep genetic divergence, consistent variation of multiple genetically independent characters, strong morphological divergence of sister clades indicating very different ecological adaptations and major differences in reproductive timing.

The existence of robust and almost completely comprehensive phylogenies for both geckos (Nielsen et al. 2011) and skinks (Chapple et al. 2009) means that it is now easy to genetically assess the identity of new specimens and the taxonomic position of those that do not match existing known species (named or unnamed). However, expert judgement and consideration of a range of contextual information are also necessary for decisions about whether new discoveries represent new species. For those, such as the recently discovered Homer skink, which are the sister taxon to a clade of several existing species, the answer is immediately obvious. However, for many others, it is not. The DNA barcoding approach, where all genetic distances above a certain threshold for that group are considered to represent distinct species, has not been found to work easily for New Zealand lizards (Chapple and Ritchie 2013). There is a very broad ‘grey zone’ of genetic distances, within which some pairs of sister taxa appear to meet the biological criteria for separate species status whilst others do not. For example, many of the long-recognised species of *Naultinus* are separated by genetic distances similar to those found among conspecific populations of other New Zealand geckos (Nielsen et al. 2011). However, the evidence for their species status is quite strong; they differ substantially in secondary sexual colouration of the males (in contrast there is no sexual colour dimorphism in the other New Zealand gecko genera), in timing of reproductive events and in body size, and based on the few examples remaining in the wild, they appear to meet at narrow contact zones where there may be some introgressive hybridisation without a loss of distinct identities between species. An example has been found recently at the Denniston and Stockton Plateaus, where *N. tuberculatus* and *N. stellatus* are both present (M. Lettink pers. comm.). It does not help that we are now making inferences from very fragmented populations, so the contact zones between them often no longer exist.

There is currently no paid full-time taxonomic herpetologist in New Zealand (and there has not been one since Charles McCann; McCann 1955), and species descriptions are either being prepared by unpaid enthusiasts or by people who have to fit this task around a very busy schedule of other work. Although a great deal of progress has been made on the taxonomy of both geckos and skinks, many unanswered questions remain for both groups, and the high likelihood of new discoveries means that the expertise of herpetological taxonomists will be required in New Zealand for a long time to come. New genetic approaches, such as the assessment of large numbers of single nucleotide polymorphisms (SNPs), are rapidly becoming more affordable and could, in future, be very useful for addressing the remaining questions, and any new questions that may arise as additional species are recognised.

Taxonomic research requires access to specimens, and the requirements of formal taxonomic description and naming usually require that a type specimen or specimens are lodged in one of the major museums. High-quality digital photographs and the ability to extract DNA from tiny skin or tail-tip biopsies mean that large-scale collecting is no longer as important for preliminary assessment of taxonomic status. However, if a new species is to be described, a type specimen or, more usually, a series of specimens must be collected. Since all New Zealand native lizards have been protected under the Wildlife Act since 1996, this requires a permit from the Department of Conservation.

Acknowledgements We thank C. Daugherty and P. Ritchie for the advice and assistance during this project. DGC's New Zealand lizard taxonomic work was funded by a postdoctoral fellowship from the Allan Wilson Centre for Molecular Ecology and Evolution. The Marsden Fund provided financial support for preliminary gecko work by RAH. and C. Daugherty.

References

Aviss M, Lyall J (1995) Survey for the "Chesterfield" skink (*Leiolopisma* sp.) near Hokitika on the West Coast, 7–9 March 1995. Threatened Species Occasional Publication No. 8. Department of Conservation, 8p + figures

Barry M, Shanas U, Brunton DH (2014) Year-round mixed-age shelter aggregations in Duvaucel's geckos (*Hoplodactylus duvaucelii*). Herpetologica 70:395–406

Bauer AM (1990) Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). Bonn Zool Monogr 30:1–218

Bell TP, Patterson GB (2008) A rare alpine skink *Oligosoma pikitanga* n. sp. (Reptilia: Scincidae) from Llawrenny Peaks, Fiordland, New Zealand. Zootaxa 1882:57–68

Boulenger GA (1906) Descriptions of two new lizards from New Zealand. Ann Mag Nat Hist 7 (17):369–371 + plate

Brandley MC, Bragg JG, Singhal S, Chapple DG, Jennings CK, Lemmon AR, Moriarty Lemmon E, Thompson MB, Moritz C (2015) Evaluating the performance of anchored hybrid enrichment at the tips of the tree of life: a phylogenetic analysis of Australian *Eugongylus* group scincid lizards. BMC Evol Biol 15:62. doi:10.1186/s12862-015-0318-0

Chambers GK, Boon WM, Buckley TR, Hitchmough RA (2001) Using molecular methods to understand the Gondwanan affinities of the New Zealand biota: three case studies. Aust J Bot 49:377–387

Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Patterson GB (2007) A new skink species (*Oligosoma taumakae* sp. nov.; Reptilia: Scincidae) from the Open Bay Islands, New Zealand. N Z J Zool 34:347–357

Chapple DG, Ritchie PA (2013) A retrospective approach to testing the DNA barcoding method. PLoS One 8:e77882. doi:10.1371/journal.pone.0077882

Chapple DG, Patterson GB, Bell T, Daugherty CH (2008a) Taxonomic revision of the New Zealand Copper Skink (*Cyclodina aenea*: Squamata: Scincidae) species complex, with descriptions of two new species. J Herpetol 42:437–452

Chapple DG, Patterson GB, Gleeson DM, Daugherty CH, Ritchie PA (2008b) Taxonomic revision of the marbled skink (*Cyclodina oliveri*, Reptilia: Scincidae) species complex, with a description of a new species. N Z J Zool 35:129–146

Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification and systematics of the New Zealand skink fauna (Reptilia: Scincidae). Mol Phylogenet Evol 52:470–487

Chapple DG, Bell T, Chapple SNJ, Miller KA, Daugherty CH, Patterson GB (2011) Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma inconspicuum*; Reptilia: Scincidae) species complex. Zootaxa 2782:1–33

Chong NL (1999) Phylogenetic analysis of the endemic New Zealand gecko species complex *Hoplodactylus pacificus* using DNA sequences of the 16S rRNA gene. Unpublished BSc (Hons) thesis, Victoria University of Wellington, Wellington

Cope ED (1869) Observations on reptiles of the old world. Proc Acad Nat Sci Phila 20(1868):316–323

Coyne JA, Orr HA (2003) Speciation. Sinauer Associates, Sunderland, MA

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Daugherty CH, Patterson GB, Thorn CJ, French DC (1990) Differentiation of the members of the New Zealand *Leiolopisma nigriplantare* species complex (Lacertilia: Scinidae). Herpetol Monogr 4:61–76

Daugherty CH, Patterson GB, Hitchmough RA (1994) Taxonomic and conservation review of the New Zealand herpetofauna. N Z J Zool 21:317–323

Dumeril AMC, Bibron G (1836) Erpetologie generale ou histoire naturelle complete des reptiles, Vol 3. Roret, Paris, iv + 517p

Fitzinger LJ [FJ] (1861) Die ausbeute der osterreichischen naturforscher an saugethieren und reptilien wahrend der weltumsegelung Sr. Majestat Fregatte Novara Osterreichische Akademie der Wissenschaften Mathematische- naturwissenschaftliche Klasse 42:383–416

Gibson S, Penniket S, Cree A (2015) Are viviparous lizards from cool climates ever exclusively nocturnal? Evidence for extensive basking in a New Zealand gecko. Biol J Linn Soc 115:882–895

Gill BJ (1976) Aspects of the ecology, morphology and taxonomy of two skinks (Reptilia: Lacertilia) in the coastal Manawatu area of New Zealand. N Z J Zool 3:141–157

Gill B, Whitaker T (2001) New Zealand frogs and reptiles. David Bateman, Auckland

Girard C (1857) Descriptions of some new reptiles, collected by the United States Exploring Expedition, under the command of Capt. Charles Wilkes, U.S.N. Part 4: Including the species of saurians, exotic to North America. Proc Acad Nat Sci Philadelphia 1857:195–199

Greaves SNJ, Chapple DG, Gleeson DM, Daugherty CH, Ritchie PA (2007) Phylogeography of the spotted skink (*Oligosoma lineoocellatum*) and green skink (*O. chloronoton*) species complex (Lacertilia: Scincidae) in New Zealand reveals pre-Pleistocene divergence. Mol Phylogenet Evol 45:729–739

Greaves SNJ, Chapple DG, Daugherty CH, Gleeson DM, Ritchie PA (2008) Genetic divergences pre-date Pleistocene glacial cycles in the New Zealand speckled skink, *Oligosoma infrapunctatum*. J Biogeogr 35:853–864

Han D, Zhou K, Bauer AM (2004) Phylogenetic relationships among gekkotan lizards inferred from C-mos nuclear DNA sequences and a new classification of the Gekkota. Biol J Linn Soc 83:353–368

Hardy GS (1977) The New Zealand Scincidae (Reptilia : Lacertilia); a taxonomic and zoogeographic study. N Z J Zool 4:221–325

Hare KM, Hoare JM, Hitchmough RA (2007) Investigating natural population dynamics of *Naultinus manukanus* to inform conservation management of New Zealand's cryptic diurnal geckos. J Herpetol 41:81–93

Hare KM, Daugherty CH, Chapple DG (2008) Comparative phylogeography of three skink species (*Oligosoma moco*, *O. smithi*, *O. suteri*; Reptilia: Scincidae) in northeastern New Zealand. Mol Phylogenet Evol 46:303–315

Hare KM, Chapple DG, Towns DR, van Winkel D (2016) The ecology of New Zealand's lizards. Chap. 6. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hitchmough RA (1997) A systematic review of the New Zealand Gekkonidae PhD. Victoria University of Wellington, Wellington

Hitchmough RA (compiler) (2002) New Zealand threat classification system lists 2002. Threatened Species Occasional Publication 23. Department of Conservation, Wellington, 210p

Hitchmough RA, Bull L, Cromarty P (compilers) (2007) New Zealand threat classification system lists 2005. Department of Conservation, Wellington, 194p

Hitchmough RA, Hoare JM, Jamieson H, Newman D, Tocher MD, Anderson PJ, Lettink M, Whitaker AH (2010) Conservation status of New Zealand reptiles, 2009. N Z J Zool 37:203–224

Hitchmough R, Anderson P, Barr B, Monks J, Lettink M, Reardon J, Tocher M, Whitaker T (2013) Conservation status of New Zealand reptiles, 2012. New Zealand Threat Classification Series 2. Department of Conservation, Wellington, 16p

Hitchmough R, Barr B, Monks J, Lettink M, Reardon J, Tocher M, van Winkel, D, Rolfe, J (2016) Conservation status of New Zealand reptiles, 2015. Department of Conservation, Wellington, New Zealand. New Zealand Threat Classification Series. Department of Conservation, Wellington

Hoare JM, Pledger S, Nelson NJ, Daugherty CH (2007) Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. Biol Conserv 136:510–519

Jewell T (2008) A photographic guide to reptiles and amphibians of New Zealand (Photographs by R. Morris). New Holland, Auckland

Jewell T, Leschen RAB (2004) A new species of *Hoplodactylus* (Reptilia: Pygopodidae) from the Takitimu Mountains, South Island, New Zealand. Zootaxa 792:1–11

Jewell T, McFarlane L (1997) Research on grey geckos (genus *Hoplodactylus* Fitzinger, 1843) in the Hawea–Wanaka district, 5–9 May 1997. Unpublished report, Otago Conservancy, Department of Conservation, Dunedin, 73p

Lettink M, Stengs H (2014) Survey for Chesterfield skink (*Oligosoma* aff. *infrapunctatum* 'Chesterfield') in the Reefton area and Grey Valley, West Coast. Unpublished Report prepared for the Department of Conservation National Office, Wellington, 12p

Liggins L, Chapple DG, Daugherty CH, Ritchie PA (2008) A SINE of restricted gene flow across the Alpine Fault: phylogeography of the New Zealand common skink (*Oligosoma nigriplantare polychroma*). Mol Ecol 17:3668–3683

Loh G (2003) Te Kakahu skink hunt (Unpublished). Otago Conservancy, Department of Conservation, Dunedin, 4p

McCann [YM] C (1955) The lizards of New Zealand. Gekkonidae and Scincidae. Dominion Mus Bull 17:1–127

Morgan-Richards M, Rheyda Hinlo M, Smuts-Kennedy C, Innes J, Ji W, Barry M, Brunton D, Hitchmough RA (2016) Identification of a rare gecko from North Island New Zealand, and genetic assessment of its probable origin: a novel mainland conservation priority? J Herpetol 50:77–86

Neilson KA (2002) Evaporative water loss as a restriction on habitat use in endangered New Zealand endemic skinks. J Herpetol 36:342–348

Neilson KA, Duganzich D, Goetz B, Waas JR (2004) Improving search strategies for the cryptic New Zealand striped skink (*Oligosoma striatum*) through behavioural contrasts with the brown skink (*Oligosoma zelandicum*). N Z J Ecol 28:267–278

Newman DG (1982) New Zealand herpetology. In: Proceedings of a symposium held at the Victoria University of Wellington, 29–31 Jan 1980. New Zealand Wildlife Service occasional publication No. 2, 495p

Nielsen SV, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol 59:1–22

O'Neill SB, Chapple DG, Daugherty CH, Ritchie PA (2008) Phylogeography of two New Zealand lizards: McCann's skink (*Oligosoma maccanni*) and the brown skink (*O. zelandicum*). Mol Phylogenet Evol 48:1168–1177

Patterson GB (1997) South Island skinks of the genus *Oligosoma*: description of *O. longipes* n. sp. with redescription of *O. otagense* (McCann) and *O. waimatense* (McCann). J R Soc N Z 27:439–450

Patterson G, Bell T (2009) The Barrier skink *Oligosoma judgei* n.sp. (Reptilia: Scincidae) from the Darran and Takitimu Mountains, South Island, New Zealand. Zootaxa 2271:43–56

Patterson GB, Daugherty CH (1990) Four new species and one new subspecies of skinks, genus *Leiolopisma* (Reptilia: Lacertilia: Scincidae) from New Zealand. J R Soc N Z 20:65–84

Patterson GB, Daugherty CH (1994) *Leiolopisma stenotis* n. sp., (Reptilia: Lacertilia: Scincidae) from Stewart Island. J R Soc N Z 24:125–132

Patterson GB, Daugherty CH (1995) Reinstatement of the genus *Oligosoma* (Reptilia: Lacertilia: Scincidae). J R Soc N Z 25:327–331

Patterson GB, Hitchmough RA, Chapple DG (2013) Taxonomic revision of the ornate skink (*Oligosoma ornatum*; Reptilia: Scincidae) species complex from northern New Zealand. Zootaxa 3736:54–68

Pickard CR, Towns DR (1988) Atlas of the amphibians and reptiles of New Zealand. Conservation Sciences Publication No. 1, Department of Conservation, Wellington

Pyron RA, Burbrink FT, Wiens JJ (2013) A phylogeny and updated classification of Squamata, including 4161 species of lizards and snakes. BMC Evol Biol 13:93

Robb J (1970) A new skink of the genus *Leiolopisma* from New Zealand. Proceedings of the Section of Sciences, Koninklijke Nederlandse Akademie van Wetenschappen C73(2):228–229

Robb J (1975) Two new skinks of the genus *Leiolopisma* from New Zealand. Proceedings of the Section of Sciences, Koninklijke Nederlandse Akademie van Wetenschappen C78(5):477–484

Robb J (1977) A revision of the synonomy of three species of Leiolopismid skinks from New Zealand. Br Mus Nat Hist 31(6):303–310

Robb J (1980a) Three new species of gekkonid lizards, genera *Hoplodactylus* Fitzinger and *Heteropholis* Fischer, from New Zealand. Natl Mus N Z Rec 1:305–310

Robb J (1980b) New Zealand amphibians and reptiles in colour. Collins, Auckland, 128p

Robb J, Hitchmough RA (1980) Review of the genus *Naultinus* Gray (Reptilia: Gekkonidae). Rec Auckland Inst Mus 16:189–200

Robb J, Rowlands RPV (1977) Reinstatement of *Hoplodactylus maculatus* (Boulenger) with redescription of *H. pacificus* (Gray) (Reptilia: Squamata : Gekkonidae). Rec Auckland Inst Mus 14:133–142

Romijn RL, Nelson NJ, Monks JM (2013) Forest geckos (*Mokopirirakau* 'Southern North Island') display diurno-nocturnal activity and are not reliant on retreats. N Z J Zool 41:103–113

Shea GM (2016) History of discovery of the New Zealand lizard fauna. Chap. 2. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Skinner A, Hugall AF, Hutchinson MN (2011) Lygosomine phylogeny and the origins of Australian scincid lizards. J Biogeogr 38:1044–1058

Smith SA, Sadlier RA, Bauer AM, Austin CC, Jackman T (2007) Molecular phylogeny for the scincid lizards of New Caledonia and adjacent areas: evidence for a single origin of the endemic skinks of Tasmantis. Mol Phylogenet Evol 43:1151–1166

Steindachner F (1869) Reptilien. In: Wullerstorf-Urbair B von (ed) Reise der Osterreichischen Fregatte Novara um die Erde, in den Jahren 1857, 1857, 1859. 1(3) Staatsdruckerei, Wien

Thomas BW (1981) *Hoplodactylus rakiurae n.* sp. (Reptilia : Gekkonidae) from Stewart Island, New Zealand, and comments on the taxonomic status of *Heteropholis nebulosus* McCann. N Z J Zool 8:33–47

Tocher MD, Marshall LJ (2001) Surveys for *Hoplodactylus* aff. *granulatus*, Roys Peak and Mt Alpha, Wanaka. Conservation advisory science notes No. 344. Department of Conservation

Towns DR, Hitchmough RA, Perrott J (2016) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? Chap. 11. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Townsend AJ, de Lange PJ, Duffy CAJ, Miskelly CM, Molloy J, Norton D (2008) New Zealand threat classification system manual. Department of Conservation, Wellington, 35p

Uetz P, Hosek J (eds) (2015) The reptile database. http://www.reptile-database.org. Accessed 13 Aug 2015

Vos ME (1988) A biochemical, morphological and phylogenetic review of the genus *Cyclodina*. Unpublished Honours Thesis, Victoria University of Wellington, Wellington

Whitaker AH (1984) *Hoplodactylus kahutarae* n.sp. (Reptilia: Gekkonidae) from the Seaward Kaikoura Range, Marlborough, New Zealand. N Z J Zool 11:259–270

Whitaker AH (1991) Research on the striped gecko, *Hoplodactylus stephensi*, on Maud Island, Pelorus Sound, Marlborough, 6–12 March, 1991. N.Z. Dept. of Conservation, Nelson/Marlborough Conservancy, Nelson

Whitaker T, Hitchmough RA, Chappell R (1999) A striped gecko (*Hoplodactylus stephensi*) at Coromandel. Conservation Advisory Science Notes No. 2, 32. Department of Conservation, Wellington

Wiley EO (1981) Phylogenetics. The theory and practice of phylogenetic systematics. Wiley-Interscience, New York

Worthy TH (1987) Osteological observations on the larger species of the skink Cyclodina and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. N Z J Zool 14:219–229

Worthy TH (2016) A review of the fossil record of New Zealand lizards. Chap. 3. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Worthy TH, Holdaway RN (2002) The lost world of the Moa. Prehistoric life of New Zealand. Indiana University Press, Bloomington, IN

Chapter 5
Biogeography of New Zealand Lizards

David G. Chapple and Rodney A. Hitchmough

Abstract New Zealand has a diverse lizard fauna, comprising diplodactylid geckos and skinks and over 100 recognised species or taxa. Geckos are thought to have colonised New Zealand during the Eocene or Oligocene (40.2–24.4 mya), prior to the 'Oligocene drowning' event. In contrast, skinks reached New Zealand during the Miocene (~18.3 mya) via long-distance overwater dispersal from New Caledonia along the Lord Howe Rise and Norfolk Ridge. Investigations of the biogeography of New Zealand lizards have long been hampered by two key factors: recent range contractions and local extinctions following the successful establishment of 31 exotic mammalian species and taxonomic gaps and a limited grasp on the true diversity of the endemic lizard fauna. However, subfossil records have improved our understanding of the prehuman distributions of several previously widespread species, and intensive taxonomic activity over the last two decades has provided a more accurate estimate of lizard diversity. This enhanced knowledge has enabled the key historical processes responsible for the diversification of lizards within New Zealand to be identified. These include sea-level changes during the Pliocene–Pleistocene in northern New Zealand, the Pliocene marine inundation of the lower North Island, the impact of water barriers such as Cook Strait (separating the North and South Islands) and Foveaux Strait (separating the South Island and Stewart island), tectonic activity along the Alpine Fault and regional north–south differentiation within the South Island. We provide an updated list of 22 biogeographic categories for New Zealand lizards. We highlight that the essential framework is now in place with which to investigate the biogeographic patterns evident in the New Zealand lizard fauna and examine the processes that have created them.

Keywords Gecko • Geology • Skink • Phylogeography • Climate • Diplodactylidae • Scincidae

---

D.G. Chapple (✉)
School of Biological Sciences, Monash University, 25 Rainforest Walk, Clayton, VIC 3800, Australia
e-mail: David.Chapple@monash.edu

R.A. Hitchmough
Department of Conservation, PO Box 10-240, Wellington, New Zealand

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_5

5.1 New Zealand's Geological and Climatic History

New Zealand contains one of the most diverse lizard faunas of any cool, temperate region on Earth (Daugherty et al. 1994; Chapple et al. 2009; Nielsen et al. 2011; Hitchmough et al. 2016a). High species richness may be driven by geological and topographic diversity (Anderson and Ferree 2010), as it increases habitat heterogeneity and provides the ecological conditions that promote speciation (Coyne and Orr 2004). Similarly, climate is a key determinant of a species' distribution (Angilletta 2009; Kearney and Porter 2009; Clusella-Trullas et al. 2011). Thus, investigation and interpretation of the biogeographic patterns evident in New Zealand lizards requires a detailed understanding of the geological and climatic history of the region.

New Zealand represents a mix of old and new. It displays attributes of both a continental fragment, a result of its Gondwanan heritage, and a long-isolated oceanic archipelago (Daugherty et al. 1993; Gibbs 2006; reviewed in Wallis and Trewick 2009). New Zealand is the main emergent landmass of the largely submerged subcontinent Zealandia (93 % of it remains submerged today; Mortimer 2004; Neall and Trewick 2008; Goldberg et al. 2008; Fig. 5.1), which split off from Gondwana approximately 82 million years ago (mya) (Cooper and Millener 1993; Gibbs 2006; Landis et al. 2008; Wallis and Trewick 2009). The Tasman Sea formed around 65 mya and led to the current 1500 km isolation of New Zealand from Australia (Cooper and Millener 1993; Gibbs 2006; Campbell and Hutching 2007; Wallis and Trewick 2009). Zealandia was subsequently stretched and thinned over the next 40 myr (64–24 mya), causing a gradual subsidence of the New Zealand landmass and increased marine inundation (Gibbs 2006; Trewick et al. 2007; Landis et al. 2008; Neall and Trewick 2008; Wallis and Trewick 2009). The extent to which New Zealand became submerged (referred to as the 'Oligocene drowning'; Suggate et al. 1978; Cooper and Millener 1993; Gibbs 2006; Wallis and Trewick 2009) is an area of active debate and controversy (e.g. Trewick et al. 2007; Landis et al. 2008), but it likely persisted throughout this period as a series of low-lying islands (e.g. Cooper and Cooper 1995; Lee et al. 2009).

Modern New Zealand had its beginnings immediately following the Oligocene drowning and, like Lazarus rising, arose from the Pacific as a result of tectonic and volcanic activity (Gibbs 2006; Trewick et al. 2007; Landis et al. 2008). This rebirth also marked the start of the most tumultuous period in New Zealand's history, as due to its placement on the boundary of the Pacific and Indo-Australian plates, there has been continual tectonic uplift, predominantly along the Alpine Fault which runs SW–NE along the majority of the South Island (Gibbs 2006; Trewick et al. 2007; Landis et al. 2008). This has resulted in New Zealand becoming a land of fire and ice (Trewick and Bland 2012). The tectonic activity that became pervasive in New Zealand resulted in volcanic activity that persisted until ~13 mya in the South Island and through to the present day in the North Island (Wallis and Trewick 2009). The ever-increasing topography of the Southern Alps (>3000 m), combined with the cooling of global temperatures since the Pliocene (Markgraf et al. 1995),

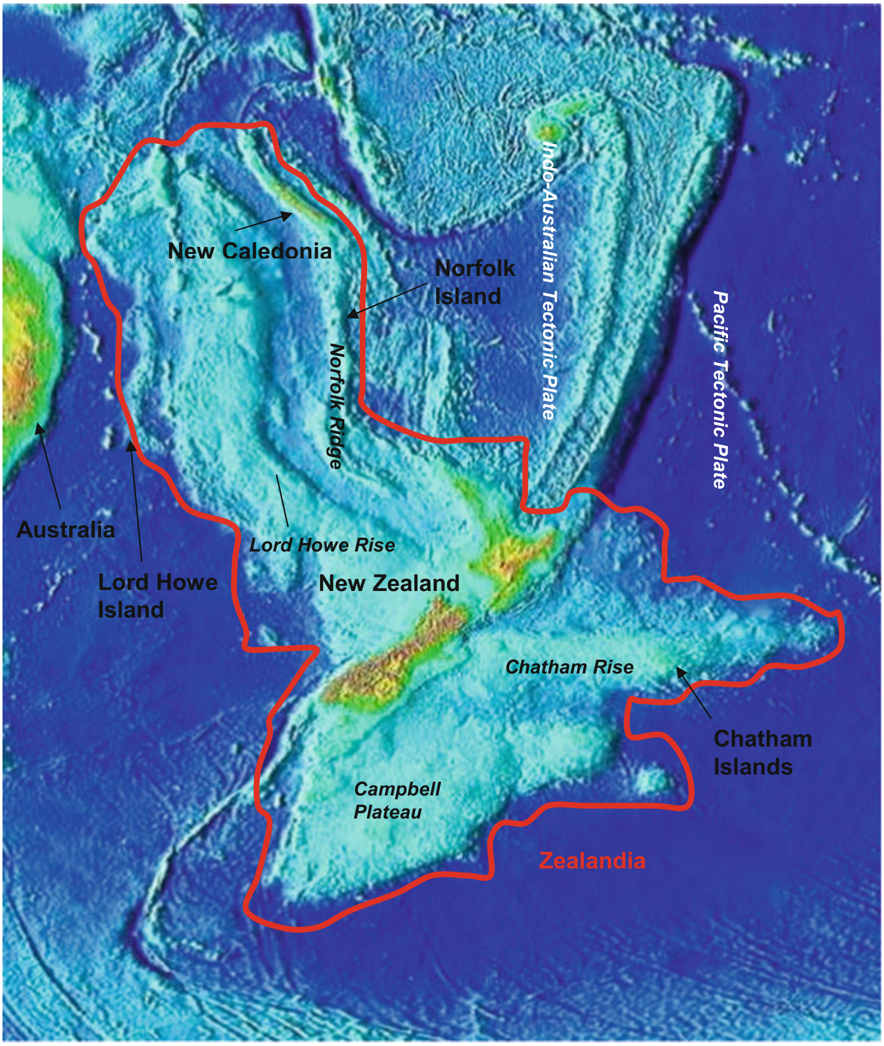


Fig. 5.1 Geographic extent of present day Zealandia (modified with Permission from Chapple et al. 2009). The *red line* indicates the approximate extent of the largely submerged continental crust of Zealandia. The locations of the Chatham Islands, Chatham Rise, Campbell Plateau, New Zealand, Lord Howe Island, Lord Howe Rise, Norfolk Island, Norfolk Ridge, New Caledonia and Australia are indicated. New Zealand is located on the boundary of the Indo-Australian and Pacific tectonic plates. The Alpine Fault refers to where this plate boundary diagonally bisects the South Island of New Zealand from the southwest to the northeast

leads to the formation of an alpine zone (Gage 1980; Suggate 1982; Stevens et al. 1995; Chamberlain et al. 1999; Lee et al. 2001; Gibbs 2006; Landis et al. 2008; Wallis and Trewick 2009). Throughout the Pliocene cooling, and the subsequent Pleistocene glacial cycles, the North Island was largely spared from extensive glaciation (Newnham et al. 1999; Carter 2005). In contrast, large swathes of the South Island (up to 30 %) were covered by glaciers during the Pleistocene (Newnham et al. 1999; Carter 2005).

Marine inundation once again became a characteristic of the New Zealand landscape during the Pliocene and Pleistocene, but on a more regional scale, and this time due to sea-level changes driven by glacial cycles (Lewis et al. 1994; Worthy and Holdaway 2002). During the Pliocene, the lower North Island was inundated, with the formation of the Manawatu Strait, which separated present-day Taranaki/Hawke's Bay from the Nelson/Marlborough region of the South Island (Bull and Whitaker 1975; Rogers 1989; Worthy and Holdaway 2002). The Pleistocene saw the formation of Cook Strait (separating North Island and South Island) and Foveaux Strait (separating South Island and Stewart Island) and the presence of an island archipelago in the Northland region (Lewis et al. 1994; Stevens et al. 1995; Worthy and Holdaway 2002). Sea-level fluctuations (up to 135 m below present levels) associated with Pleistocene glacial cycles result in the intermittent presence of land bridges across Cook Strait and Foveaux Strait and the reconnection of previously isolated regions of Northland (Lewis et al. 1994; Stevens et al. 1995; Worthy and Holdaway 2002).

Present-day New Zealand has a predominantly north–south orientation and spans 13° latitude (34–47°S; Fig. 5.2). It is situated in the Southwest Pacific and comprises two main islands (North Island, 113,729 km^2; South Island, 150,437 km^2) and Stewart Island (1680 km^2; Fig. 5.2).

5.2 Origin and Colonisation of the New Zealand Lizard Fauna

Two key, but linked, questions have polarised the field of New Zealand biogeography: (i) do particular taxa have Gondwanan or post-Gondwanan origins? and (ii) did the resident biota persist in New Zealand through the Oligocene drowning or colonise afterwards? (Waters and Craw 2006; Gibbs 2006; Trewick et al. 2007; Landis et al. 2008; Sharma and Wheeler 2013). Whilst there is strong evidence that tuatara and Leiopelmatid frogs have Gondwanan origins and were present in New Zealand throughout the Oligocene (Rest et al. 2003; Roelants and Bossuyt 2005; Hugall et al. 2007; Cree 2014), skinks (Scincidae) and geckos (Diplodactylidae) arrived in New Zealand after its separation from Gondwana (Chapple et al. 2009; Nielsen et al. 2011).

Early researchers postulated a post-Oligocene colonisation of geckos into New Zealand, with overwater dispersal in the Miocene of an Asian lineage first to Australia then to New Zealand via New Caledonia (Kluge 1967; Bull and Whitaker 1975). Several authors subsequently proposed a vicariant Gondwanan origin for New Zealand geckos (Bauer 1990; Hitchmough 1997; Chambers et al. 2001). However, recent molecular studies have indicated diplodactylid geckos

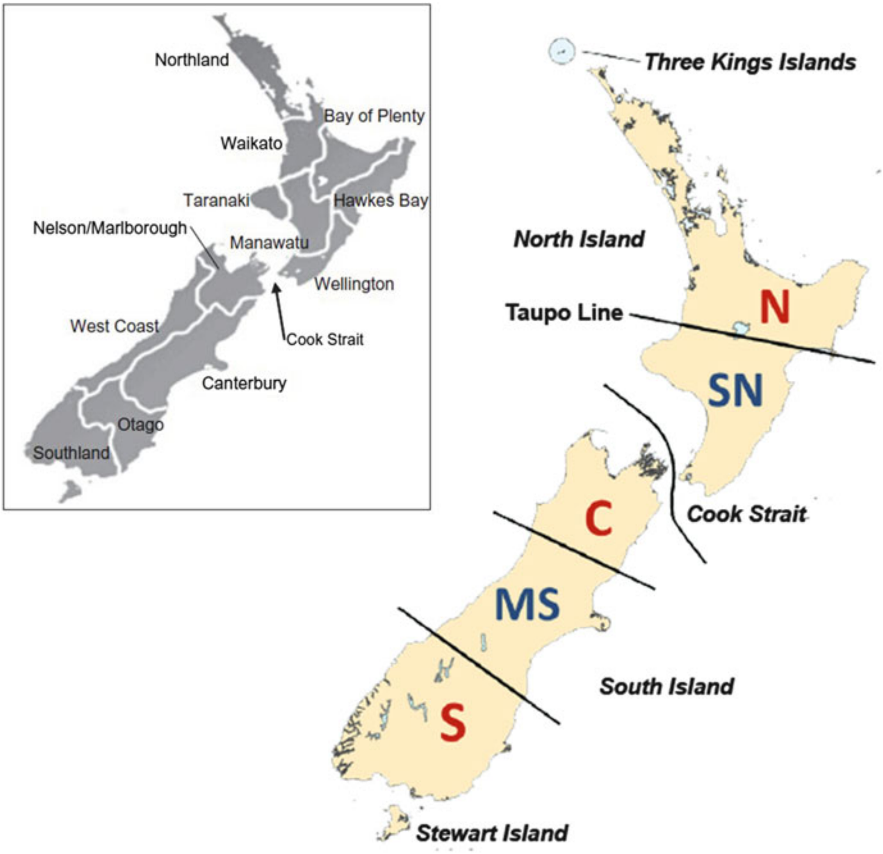


Fig. 5.2 Map of New Zealand indicating the approximate location of the Taupo line and the major biogeographic regions: N, northern North Island; SN, southern North Island; C, central New Zealand; MS, mid-South Island; and S, southern South Island (adapted with permission from Di Virgilio et al. 2014). *Inset:* major geographic regions in New Zealand (adapted with permission from O'Neill et al. 2008)

colonised New Zealand via long-distance overwater dispersal from Australia about 40.2 mya (53.5–28.9 mya) during the Eocene or Oligocene and prior to (or during) the Oligocene drowning (between 40.2 and 24.4 mya; Nielsen et al. 2011).

Similarly, skinks were initially suggested to have multiple colonisations of New Zealand, from Australia and/or Southeast Asia, during the Pliocene–Pleistocene (McCann 1955; Towns 1974; Bull and Whitaker 1975; Hardy 1977; Robb 1973, 1980). Subsequent studies based on allozymes and DNA sequence data indicated a single colonisation (from New Caledonia or the Southwest Pacific) and pushed back the arrival of skinks into New Zealand to the late Oligocene–early Miocene (~20–23 mya; Towns et al. 1985; Hickson et al. 2000; Smith et al. 2007). However, a more comprehensive molecular study (Chapple et al. 2009) indicated that Eugongylinae skinks colonised New Zealand from New Caledonia, via overwater dispersal and island hopping along the Lord Howe Rise and Norfolk Ridge, during the Miocene (18.3 mya, range 16–22.6 mya). Indeed, the St. Bathans fossil deposit confirms that both skinks and geckos were present in New Zealand during the Miocene (~19–16 mya; Lee et al. 2009; Worthy 2016).

5.3 Diversification of Lizards Within New Zealand

Lizards exhibited high rates of diversification following their colonisation of New Zealand, with skinks radiating into at least 61 species within a single genus (*Oligosoma*) and geckos into at least 43 species across seven genera (*Dactylocnemis*, *Hoplodactylus*, *Mokopirirakau*, *Naultinus*, *Toropuku*, *Tukutuku* and *Woodworthia*; Hitchmough et al. 2016a, b). Two key factors have acted to obscure our understanding of the diversification and spread of New Zealand lizards. First, the introduction of a diverse array of mammals into New Zealand, an archipelago that was previously largely devoid of terrestrial mammals (Worthy and Holdaway 2002; Worthy et al. 2006), resulted in widespread range contractions of numerous lizard species (Towns et al. 1985, 2016; Tingley et al. 2013; Nelson et al. 2015; Hitchmough et al. 2016b). This alteration of geographic ranges has restricted our capacity to grasp biogeographic patterns of New Zealand lizards, although molecular or fossil data can often be used to reconstruct these prehuman distributions of native lizard species (Worthy and Holdaway 2002; Chapple et al. 2008a; Lee et al. 2009; Worthy 2016). Secondly, gaps in taxonomic knowledge, pronounced until recently (Hitchmough et al. 2016a), have masked the true lizard diversity present in New Zealand. For instance, numerous regions of the country have yet to be explored in detail to assess their lizard diversity. Expeditions that have been conducted to remote areas of the South Island (e.g. Jewell and Tocher 2005; Jewell 2007) have uncovered several new lizard species (Chapple and Patterson 2007; Bell and Patterson 2008; Patterson and Bell 2009; Chapple et al. 2011). Furthermore, a large proportion of New Zealand's known lizard diversity (45 %) is yet to be formally described (Hitchmough et al. 2016a, b).

Despite these hurdles, numerous studies over the last decade have investigated the biogeographic and phylogeographic patterns evident in New Zealand lizards. Published studies have focused predominantly on skinks (Berry and Gleeson 2005; Chapple and Patterson 2007; Greaves et al. 2007, 2008; Hare et al. 2008; Liggins et al. 2008a, b; O'Neill et al. 2008; Chapple et al. 2008a, b, c, 2009, 2011, 2012; Miller et al. 2009; Patterson et al. 2013; Di Virgilio et al. 2014; Nelson-Tunley et al. 2016), with less attention paid to geckos (Towns et al. 1985; Nielsen et al. 2011; Di Virgilio et al. 2014). These studies have demonstrated that the New Zealand lizard fauna is characterised by continental-level biogeographic patterns (e.g. deep genetic splits) over relatively short geographic distances, the result of strong regional tectonic or eustatic processes (e.g. uplift along Alpine Fault; marine inundation associated with tectonic activity or glacial cycles), combined with strong gradients over short distances in altitude, rainfall, vegetation and substrate. Diversification of both skinks and geckos has occurred across several periods, namely, the mid–late Miocene, the late Miocene–Pliocene and the Pliocene–Pleistocene (Chapple et al. 2009; Nielsen et al. 2011). This has resulted in nine key biogeographic patterns within the New Zealand lizard fauna.

5.3.1 Non-land-bridge Northern Island Groups

Most New Zealand islands, along with all three main islands, were connected in a single large landmass when sea levels dropped during the Pleistocene glaciations. However, some groups lying in deeper water continued to be isolated as islands throughout that period. These include the Three Kings and Poor Knights and possibly the Mokohinaus/Pokohinaus, at least for most of the time. These three groups (particularly the first two) have high levels of endemism in their lizard faunas. For the Three Kings, two of its six resident lizard species are endemic, for the Mokohinaus one of seven; for the Poor Knights, three of eight species. In addition, other populations on these islands such as the Poor Knights Islands population of *O. oliveri* and the Three Kings Islands population of *O. ornatum* have diverged in body size and/or morphology from other populations of the species. The more distantly isolated New Zealand island groups, the Kermadecs in the subtropics and the various subantarctic island groups, have never had any records of terrestrial reptiles. Apparent endemism of lizards on other land-bridge islands is now understood to be secondary to the effects of invasive mammals causing extinctions of those species on the mainland where they were widespread before human settlement.

5.3.2 Northland Diversification

Sea-level changes during the Pliocene–Pleistocene modified the landscape of Northland, with the repeated connection, and subsequent isolation, of offshore islands (Rogers 1989; King 2000; Worthy and Holdaway 2002). At its extreme, island groups such as the Poor Knights and Three Kings have been separated from the North Island mainland for up to 1–2 myr (Hayward 1986, 1991). These sea-level fluctuations appear to have resulted in substantial diversification in both skinks (Chapple et al. 2008a, b, c, 2009; Hare et al. 2008; Patterson et al. 2013) and geckos (*Dactylocnemis* and *Naultinus*; Nielsen et al. 2011). Three undescribed geckos and a skink are endemic to the Aupori or Aupouri, plus Karikari Peninsulas. However, as of yet, there has been little consistency in terms of the timing and placement of biogeographic breaks across taxonomic groups (Wallis and Trewick 2009).

5.3.3 Taupo Line Biogeographic Barrier

A substantial discontinuity in lizard distributions occurs across a line (referred to as the Taupo line) which roughly follows the axial ranges in the East Cape area, then passes just south of Lake Taupo, north of Tongariro National Park and then south through the King Country and inland Taranaki to meet the coast somewhere west of Whanganui (Fig. 5.2). The Taupo line represents a significant species transition zone, with relatively few species possessing distributions that span this boundary (McCann 1955; Chapple et al. 2009). The distributional boundaries of all the lizard species involved do not coincide exactly, but all roughly follow this line. *N. elegans, M. granulatus, D. pacificus*, *O.* aff. *infrapunctatum* 'crenulate', *O. striatum* and the eastern coastal endemic skinks *O. suteri, O. moco* and *O. smithii* are found only north and west of this line, whereas *N. punctatus, M.* 'southern North Island', inland populations of *W. maculata*, *O. lineoocellatum, O. polychroma* and *O.* aff. *infrapunctatum* 'southern North Island' are found only south and east of this line (McCann 1955, 1956; Hare et al. 2008; Liggins et al. 2008a; Chapple et al. 2009; Nielsen et al. 2011). In fact no gecko species currently with viable mainland populations crosses this line, except for *W. maculata*, which is widespread inland south of the line, but in the north is confined to coastal habitats. *H. duvaucelii* also spans the line (and Cook Strait) but is currently almost entirely confined to mammal-free offshore islands. Populations on islands in Cook Strait form a distinct clade and are also diagnostically different in morphology from northern populations (Morgan-Richards et al. 2016).

The Taupo line is located near the northern edge of where the Manawatu Strait was located during the Pliocene (Bull and Whitaker 1975; Rogers 1989; Worthy and Holdaway 2002). If this contact zone represents secondary contact following isolation across the Pliocene Manawatu Strait, the species meeting there might be expected to be sister taxa and to have similar depths of genetic divergence, reflecting the age of the isolation event. In contrast, none of the congeneric gecko pairs or ecologically similar or closely related skink pairs are sister species, and depths of genetic divergence between them cover a very broad spectrum, from 24.4 ± 8.9 mya for *D. pacificus* and *W. maculata* to <1 mya for *N. elegans* and *N. punctatus* (Nielsen et al. 2011). The depth of divergence in *M.* is intermediate between these extremes. *M.* 'southern North Island' is sister to the remainder of the genus, whilst more *M. granulatus* has recently colonised the North Island from the South Island (Nielsen et al. 2011). The skinks show similar patterns, with those north and south of the line mostly separated by the deepest split in the New Zealand skink radiation. However, the two North Island taxa of the *O. infrapunctatum* complex appear to represent independent colonisations of the North Island by different South Island ancestors (Greaves et al. 2008).

5.3.4 Cook Strait

Cook Strait is the shallow waterway that separates the present-day North and South Islands (Fig. 5.2). However, during Pleistocene glacial cycles, land bridges linking the two islands were present intermittently, potentially facilitating the movement of lizards across this region (Lewis et al. 1994; Worthy and Holdaway 2002). The evidence for dispersal across these Cook Strait land bridges varies among species, with genetic studies indicating recent dispersal between the two islands in several skink species (*O. zelandicum, O. maccanni*, *O. infrapunctatum*, *O. lineoocellatum*, *O. polychroma*; Greaves et al. 2007, 2008; O'Neill et al. 2008; Liggins et al. 2008a). Similarly, the current distribution of several gecko species (*M. granulatus*, *W. maculata, W.* 'Marlborough mini', *H. duvaucelii*) and pattern of genetic variation within them are also suggestive of linkages across Cook Strait (Hitchmough 1997; Nielsen et al. 2011). In contrast, Cook Strait represents a distributional barrier for several skink (e.g. *O. aeneum*, *O. ornatum*, *O. whitakeri*; Chapple et al. 2008a, 2009; Miller et al. 2009) and gecko species (e.g. *Naultinus* spp., *W. chrysosiretica*, probably *Toropuku stephensi*; Nielsen et al. 2011) (Figs. 5.3 and 5.4). Intriguingly, skink species that are continuously distributed across the Taupo line are less likely to have distributions that span Cook Strait, and vice versa (reviewed in Chapple et al. 2009; Fig. 5.4); this does not apply to geckos.

5.3.5 Alpine Fault

The Southern Alps, located along the Alpine Fault in the South Island, have experienced dramatic topographic uplift since the Miocene. This tectonic activity appears to have driven east–west biogeographic breaks (of Miocene–Pliocene origin) in several skink (*O. polychroma*, Liggins et al. 2008a; *O. lineoocellatum*, Greaves et al. 2007) and gecko species (*Mokopirirakau*, *Naultinus*; Nielsen et al. 2011). This has led to many individual lizard species exhibiting distributions that are restricted entirely to the east, or to the west, of the Southern Alps (Chapple et al. 2009; Nielsen et al. 2011; Figs. 5.3 and 5.4). Indeed, most species with ranges spanning Cook Strait are widely distributed across the North Island, but are restricted to the western side of the Southern Alps in the South Island (Table 5.1; Figs. 5.3 and 5.4). *Woodworthia*, despite having its highest diversity immediately east of the Southern Alps, is almost entirely absent to the west.

5.3.6 North–South Splits in the South Island

One of the earliest biogeographic patterns that was characterised in the New Zealand biota was the alternating extremes of high and low endemism in the

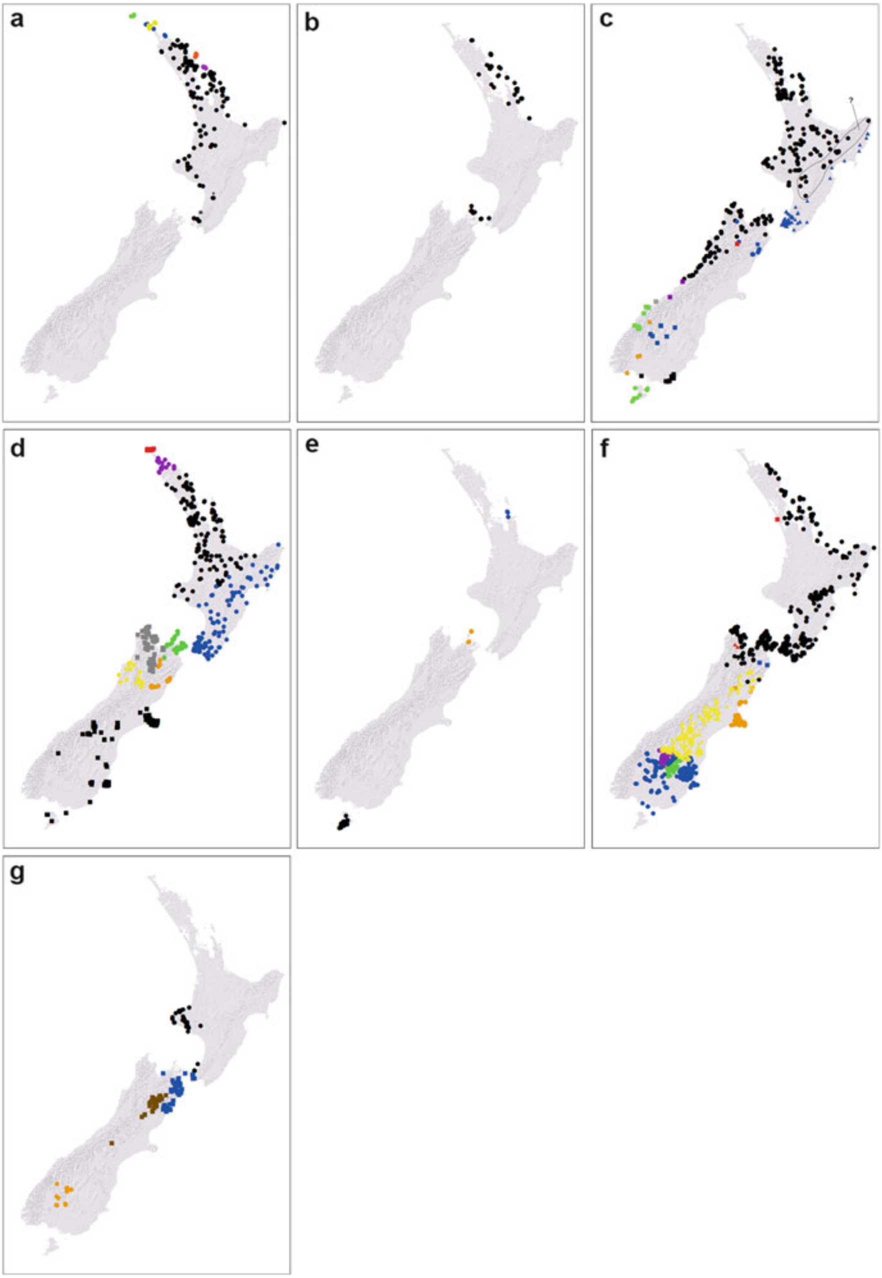


Fig. 5.3 Distribution of New Zealand gecko species. The distributional data follows the Department of Conservation BioWeb Herpetofauna database (used with permission from Benno Kappers, Department of Conservation). (**a**) ***Dactylocnemis***: *D. pacificus* (*black*; note that the records in the southern North Island marked with an *asterisk* are probably the result of human-assisted transport), *D*. 'Matapia Island' (*blue*), *D*. 'Mokohinau' (*purple*), *D*. 'North Cape' (*yellow*), *D*. 'Poor Knights'

eastern South Island from Nelson–Marlborough (high), Canterbury (low) and Otago–Southland (high) (Wardle 1991; Wardle et al. 1988; Craw 1989; Gibbs 2006) (a similar pattern is seen on the West Coast). This is thought to be due to a combination of tectonic activity and climatic processes (e.g. Pleistocene glacial cycles). In lizards, this appears to have resulted in biogeographic breaks, at both the intra- and interspecific level, in skinks (e.g. *O. polychroma*, *O. maccanni*, *O. chloronoton–lineoocellatum*, *O. otagense–waimatense*; Greaves et al. 2007; O'Neill et al. 2008; Liggins et al. 2008a; Chapple et al. 2012) and geckos (*Naultinus*, *Woodworthia*; Nielsen et al. 2011). The pattern of reduced endemism in Canterbury noted for other biotic groups is less true for the lizards: Marlborough has eight endemic species or deeply divergent intraspecific clades (*N. manukanus, N. rudis, W.* 'Marlborough mini'*, W.* 'Kaikouras'*, O. longipes* sensu stricto*, O.* aff. *polychroma* clades 2 and 3, *O.* aff. *lineoocellatum* clade 2a and in addition *W. maculata* and *M. kahutarae* are found in Marlborough but not in Canterbury), Canterbury six (*W.* cf. *brunnea, O.* aff. *longipes* 'southern', *O.* aff. *longipes* 'Rangitata', *O.* aff. *polychroma* clade 4, *O.* aff. *lineoocellatum* clades 2b and 2c) and Otago–Southland thirteen (*W.* 'Otago/Southland large', *W.* 'Cromwell', *W.* 'Central Otago', *W.* 'southern mini', *O. otagense, O. grande, O. inconspicuum, O. burganae, O. repens, O. toka, O.* aff. *chloronoton* clades 3a, 3b and 3c). A much smaller number of species span these boundaries: *W.* 'Southern Alps' extends from Canterbury well into South Marlborough, as does *O. waimatense* (although with deeply divergent southern and northern clades), and *W.* 'pygmy' extends from south Marlborough well south into Canterbury. *N. gemmeus* and *O.* aff. *polychroma* clade 5 extend across Otago/Southland and much of Canterbury, as does *O. maccanni*, but in the latter case with much deeper intraspecific genetic structuring. There are also a few unconfirmed sightings and sloughed skins of *Mokopirirakau* from the eastern South Island, but their history and taxonomic identity are unknown so they are not considered here.

Fig. 5.3 (continued) (*orange*), *D.* 'Three Kings' (*green*). (**b**) ***Hoplodactylus***: *H. duvaucelii* (*black*). (**c**) ***Mokopirirakau***: *M. cryptozoicus* (*orange circles*), *M. granulatus* (*black circles*), *M. kahutarae* (*blue circles*), *M. nebulosus* (*green circles*), *M.* 'Cascades' (*green squares*), *M.* 'cupola' (*red square*), *M.* 'Okarito' (*purple squares*), *M.* 'Open Bay Islands' (*grey squares*), *M.* 'Roys Peak' (*blue squares*) *M.* 'southern forest' (*black squares*), *M.* 'southern NI' (*blue triangles*). Note that the taxonomic affinities of some populations in the North Island (as highlighted) are unknown. (**d**) ***Naultinus***: *N. elegans* (*black circles*), *N. gemmeus* (*black squares*), *N. grayii* (*purple circles*), *N. manakanus* (*green circles*), *N. punctatus* (*blue circles*), *N. rudis* (*orange circles*), *N. stellatus* (*grey squares*), *N. tuberculatus* (*yellow circles*), *N.* 'North Cape' (*red squares*). (**e**) ***Toropuku* and *Tukutuku***: *Toropuku stephensi* (*orange*), *Toropuku* 'Coromandel' (*blue*), *Tukutuku rakiurae* (*black*). (**f**) ***Woodworthia* (part 1)**: *W. maculata* (*black circles*), *W.* 'Central Otago' (*green circles*), *W.* 'Cromwell' (*purple circles*), *W.* 'Kaikouras' (*blue squares*), *W.* 'Mount Arthur' (*red triangles*), *W.* 'Otago/Southland large' (*blue circles*), *W.* 'Southern Alps' (*yellow triangles*), *W.* aff. *maculata* 'Muriwai' (*red square*), *W.* c.f. *brunnea* (*orange circles*). (**g**) ***Woodworthia* (part 2)**: *W. chrysosiretica* (*black circles*), *W.* 'Marlborough mini' (*blue squares*), *W.* 'pygmy' (*brown square*), *W.* 'southern mini' (*orange circle*)

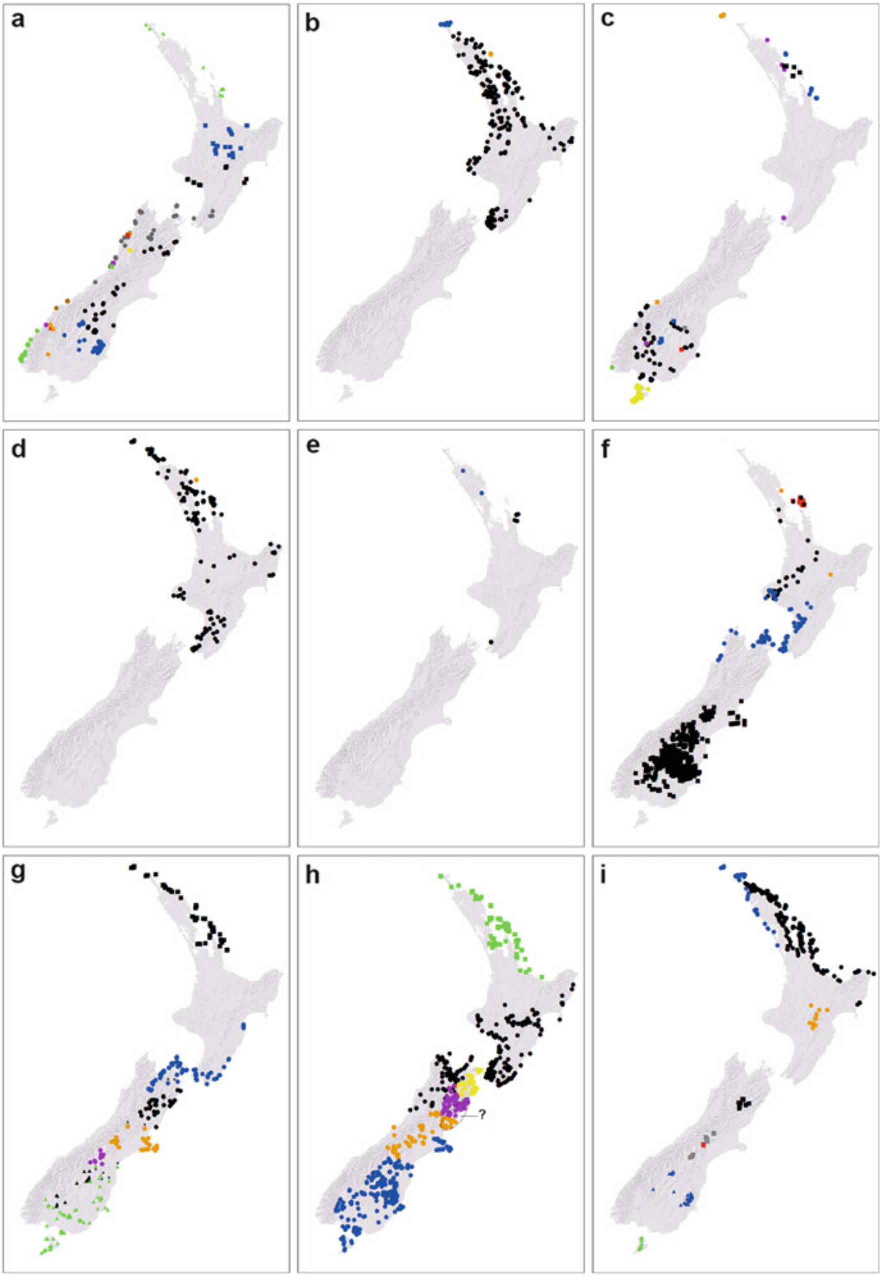


Fig. 5.4 Distribution of New Zealand skink species. The distributional data follows the Department of Conservation BioWeb Herpetofauna database (used with permission from Benno Kappers, Department of Conservation). (**a**) **Clade 2 +** ***O. alani***: *O. alani* (*green triangles*), *O. infrapunctatum* (*grey circles*), *O.* aff. *infrapunctatum* 'crenulate' (*blue squares*), *O.* aff. *infrapunctatum* 'southern North Island' (*black squares*), *O.* aff. *infrapunctatum* 'Alborn' (*yellow squares*), *O.* aff. *infrapunctatum* 'Chesterfield' (*purple squares*), *O.* aff. *infrapunctatum* 'cobble' (*orange square*), *O.* aff. *infrapunctatum* 'Hokitika' (*green square*), *O.* aff. *infrapunctatum*

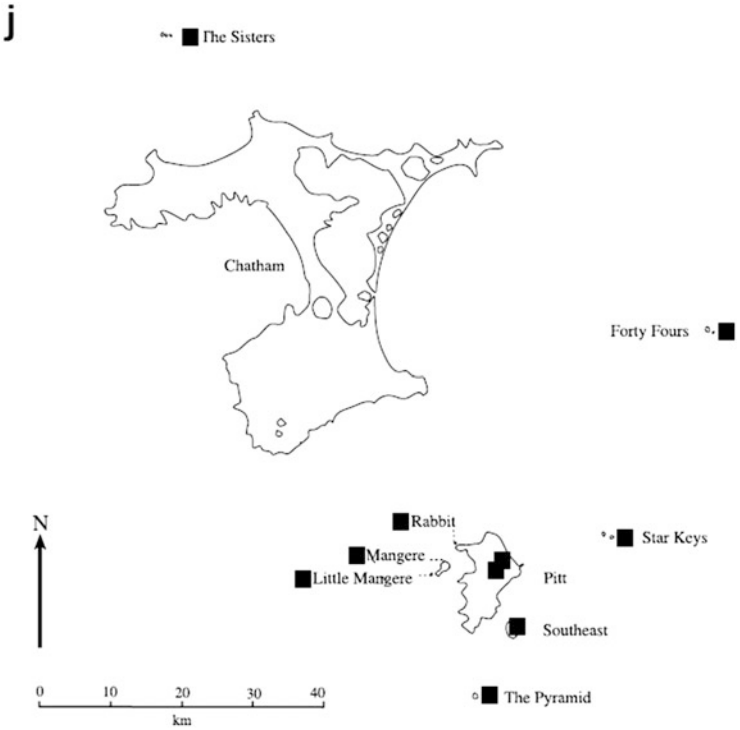


Fig. 5.4 (continued) 'Westport' (*red square*), *O. waimatense* (*black circles*), *O. otagense* (*blue circles*), *O. acrinasum* (*green circles*), *O. judgei* (*orange circles*), *O. pikitanga* (*purple circles*), *O. taumakae* (*brown circles*), *O.* sp. 'Homer Tunnel' (*red triangle*). (**b**) **Clade 3**: *O. aeneum* (*black circles*), *O. hardyi* (*orange circles*), *O. levidensum* (*blue circles*). (**c**) **Clade 4 (part 1) +** ***O. inconspicuum*** **complex**: *O. fallai* (*orange circles*), *O. macgregori* (*purple circles*), *O. oliveri* (*blue circles*), *O. townsi* (*black squares*), *O. burganae* (*red squares*), *O. inconspicuum* (*black circles*), *O. notosaurus* (*yellow circles*), *O. repens* (*purple square*), *O. tekakahu* (*green circles*), *O. toka* (*blue squares*), *O.* aff. *inconspicuum* 'North Otago' (*grey squares*), *O.* aff. *inconspicuum* 'Okuru' (*orange squares*). (**d**) **Clade 4 (part 2):** *O. ornatum* (*black circles*), *O. roimata* (*orange circles*). (**e**) **Clade 4 (part 3):** *O. whitakeri* (*black circles*), *O. northlandi* (extinct; *blue circles*). (**f**) **Clade 5 +** ***O. maccanni*****:** *O. zelandicum* (*blue circles*), *O. striatum* (*black circles*), *O. homalonotum* (*red squares*), *O.* 'Whirinaki' (*orange circles*), *O. maccanni* (*black squares*). (**g**) **Clade 6 +** ***O. lineoocellatum–O. chloronoton*** **complex:** *O. suteri* (*black squares*), *O. lineoocellatum* (*blue circles*), *O.* aff. *lineoocellatum* 'South Marlborough' (*black circles*), *O.* aff. *lineoocellatum* 'Central Canterbury' (*orange circles*), *O.* aff. *lineoocellatum* 'Mackenzie Basin' (*purple circles*), *O. chloronoton* (*green triangles*), *O.* aff. *chloronoton* 'West Otago' (*black triangles*). The *asterisks* indicate populations where the taxonomic affinities are uncertain. (**h**) **Clade 7 +** ***O. polychroma*** **complex:** *O. moco* (*green squares*), *O. polychroma* (*black circles*), *O. polychroma* clade 2 (*yellow circles*), *O. polychroma* clade 3 (*purple circles*), *O. polychroma* clade 4 (*orange circles*), *O. polychroma* clade 5 (*blue circles*). Note that the taxonomic affinities of some populations in the Kaikoura area south to Christchurch (as highlighted) are unknown. Clades 4 and 5 may be sympatric in the Lindis Pass–Mackenzie Basin region. (**i**) **Clade 8 +** ***O. grande*****,** ***O. stenotis*****,** ***O. longipes*** **complex:** *O. smithi* (*black circles*), *O.* aff. *smithi* 'Three Kings, Te Paki, western Northland' (*blue circles*), *O. microlepis* (*orange circles*), *O. grande* (*blue triangles*), *O. stenotis* (*green triangles*), *O. longipes* (*black squares*), *O.* aff. *longipes* 'southern' (*grey squares*), *O. longipes* 'Rangitata' (*red squares*). (**j**) ***O. nigriplantare***: distribution within the Chatham Islands. Note that it does not occur on the main Chatham Island (modified with permission from Liggins et al. 2008b)

Table 5.1 Biogeographic categories for New Zealand skinks and geckos [adapted and modified from Towns et al. (1985)]

Species	Biogeographic category
Skinks (Scincidae: Eugongylinae)	
Oligosoma acrinasum (Hardy, 1977)	17
Oligosoma aeneum (Girard, 1857)	4
Oligosoma alani (Robb, 1970)	3
Oligosoma burganae (Chapple et al. 2011)	19
Oligosoma chloronoton (Hardy, 1977)	16
Oligosoma aff. *chloronoton* 'West Otago'	15
Oligosoma fallai (McCann, 1955)	1
Oligosoma grande (Gray, 1845)	15
Oligosoma hardyi (Chapple et al. 2008)	1
Oligosoma homalonotum (Boulenger, 1906)	3
Oligosoma inconspicuum (Patterson & Daugherty, 1990)	16
Oligosoma aff. *inconspicuum* 'North Otago'	15
Oligosoma aff. *inconspicuum* 'Okuru'	17
Oligosoma infrapunctatum (Boulenger, 1887)	10
Oligosoma aff. *infrapunctatum* 'Alborn'	11
Oligosoma aff. *infrapunctatum* 'Chesterfield'	11
Oligosoma aff. *infrapunctatum* 'cobble'	11
Oligosoma aff. *infrapunctatum* 'crenulate'	7
Oligosoma aff. *infrapunctatum* 'Hokitika'	11
Oligosoma aff. *infrapunctatum* 'southern North Island'	8
Oligosoma aff. *infrapunctatum* 'Westport'	11
Oligosoma judgei (Patterson & Bell, 2009)	19
Oligosoma levidensum (Chapple et al., 2008)	5
Oligosoma lineoocellatum (Duméril & Duméril, 1851)	10
Oligosoma aff. *lineoocellatum* 'Central Canterbury'	14
Oligosoma aff. *lineoocellatum* 'Mackenzie Basin'	14
Oligosoma aff. *lineoocellatum* 'South Marlborough'	12
Oligosoma longipes (Patterson, 1997)	12
Oligosoma aff. *longipes* 'Rangitata'	14
Oligosoma aff. *longipes* 'southern'	14
Oligosoma maccanni (Patterson & Daugherty, 1990)	18
Oligosoma macgregori (Robb, 1975)	9
Oligosoma microlepis (Patterson & Daugherty, 1990)	7
Oligosoma moco (Duméril & Bibron, 1839)	2
Oligosoma nigriplantare (Peters, 1873)	22
Oligosoma notosaurus (Patterson & Daugherty, 1990)	21
Oligosoma oliveri (McCann, 1955)	3
Oligosoma ornatum (Gray, 1843)	4
Oligosoma otagense (McCann, 1955)	15
Oligosoma pikitanga (Bell & Patterson, 2008)	19
Oligosoma polychroma (Patterson & Daugherty, 1990)	10

(continued)

Table 5.1 (continued)

Species	Biogeographic category
Oligosoma aff. *polychroma* clade 2	12
Oligosoma aff. *polychroma* clade 3	12
Oligosoma aff. *polychroma* clade 4	14
Oligosoma aff. *polychroma* clade 5	16
Oligosoma repens (Chapple et al. 2011)	19
Oligosoma roimata (Patterson, Hitchmough & Chapple, 2013)	1
Oligosoma smithi (Gray, 1845)	2
Oligosoma aff. *smithi* “Three Kings, Te Paki, Western Northland’	2
Oligosoma stenotis (Patterson & Daugherty, 1994)	21
Oligosoma striatum (Buller, 1871)	7
Oligosoma suteri (Boulenger, 1906)	2
Oligosoma taumakae (Chapple & Patterson, 2007)	17
Oligosoma tekakahu (Chapple et al. 2011)	17
Oligosoma toka (Chapple et al. 2011)	19
Oligosoma townsi (Chapple et al. 2008)	3
Oligosoma waimatense (McCann, 1955)	13
Oligosoma whitakeri (Hardy, 1977)	9
Oligosoma zelandicum (Gray, 1843)	10
Oligosoma ‘Whirinaki’	7
Oligosoma sp. ‘Homer Tunnel’	19
Geckos (Diplodactylidae)	
Dactylocnemis pacificus (Gray, 1842)	4
Dactylocnemis ‘Matapia Island’	5
Dactylocnemis ‘Mokohinau’	1
Dactylocnemis ‘North Cape’	5
Dactylocnemis ‘Poor Knights’	1
Dactylocnemis ‘Three Kings’	1
Hoplodactylus duvaucelii (Duméril & Bibron, 1836)	9
Mokopirirakau cryptozoicus (Jewell & Leschen, 2004)	16
Mokopirirakau granulatus (Gray, 1845)	10
Mokopirirakau kahutarae (Whitaker, 1985)	12
Mokopirirakau nebulosus (McCann, 1955)	21
Mokopirirakau ‘Cascades’	17
Mokopirirakau ‘Cupola’	12
Mokopirirakau ‘Okarito’	11
Mokopirirakau ‘Open Bay Islands’	17
Mokopirirakau ‘Roys Peak’	15
Mokopirirakau ‘southern forest’	20
Mokopirirakau ‘southern North Island’	8
Naultinus elegans (Gray, 1842)	6
Naultinus gemmeus (McCann, 1955)	18
Naultinus grayii (Bell, 1843)	5

(continued)

Table 5.1 (continued)

Species	Biogeographic category
Naultinus manukanus (McCann, 1955)	12
Naultinus punctatus (Gray, 1842)	8
Naultinus rudis (Fischer, 1882)	12
Naultinus stellatus (Hutton, 1872)	12
Naultinus tuberculatus (McCann, 1955)	11
Naultinus 'North Cape'	5
Toropuku stephensi (Robb, 1980)	12
Toropuku 'Coromandel'	7
Tukutuku rakiurae (Thomas, 1981)	21
Woodworthia chrysosiretica (Robb, 1980)	7
Woodworthia maculata (Gray, 1845)	10
Woodworthia aff. *maculata* 'Muriwai'	2
Woodworthia 'Central Otago'	15
Woodworthia 'Cromwell'	15
Woodworthia 'Kaikouras'	12
Woodworthia 'Marlborough mini'	10
Woodworthia 'Mount Arthur'	12
Woodworthia 'Otago/Southland large'	16
Woodworthia 'pygmy'	14
Woodworthia 'Southern Alps'	18
Woodworthia 'southern mini'	15
Woodworthia cf. *brunnea*	14

The taxonomic authority for described species is provided. The geographic distribution of each species is provided in Figs. 5.3 and 5.4. The 22 biogeographic categories are (1) northern island endemic, (2) northern coastal, (3) northern island relicts, (4) widespread North Island, (5) northern Northland, (6) northern North Island, (7) central North Island, (8) southern North Island, (9) disjunctive relicts, (10) span Cook Strait, (11) West Coast endemic, (12) Nelson/Marlborough endemic, (13) Marlborough/Canterbury, (14) Canterbury endemic, (15) Otago endemic, (16) Otago/Southland, (17) South Westland/Fiordland coastal/island endemic, (18) widespread South Island, (19) southern montane/alpine endemic, (20) Southland endemic, (21) Stewart Island endemic, (22) Chatham Islands endemic

The boundary between Otago and Canterbury is in the Waitaki Valley; all lizard species distributed across this boundary show at least changes in colour. Many pairs of parapatric sister species meet there, but in *O. maccanni*, the boundary is intraspecific between subclades, and in *O. polychroma* and *N. gemmeus*, there is an abrupt change in colour with little or no divergence in neutral genetic markers. The sister taxon relationships across the Waitaki Valley are in contrast to the Taupo line, but as with the Taupo line, their dates of divergence differ considerably, indicating that the processes driving the formation of this zone were not drivers of the original speciation events.

5.3.7 East–West Splits in Otago

Active since the late Miocene, the Nevis–Cardrona fault system (delineated by the Cardrona and Nevis rivers) represents the border between eastern and western Otago (reviewed in Waters et al. 2001). Deep genetic breaks are evident across this region in several skink species (*O. grande*, *O. maccanni*, *O. otagense*; Berry and Gleeson 2005; O'Neill et al. 2008; Chapple et al. 2012), and species level breaks are also present in *Woodworthia* geckos (Nielsen et al. 2011). Similarly, tectonic activity in the southern South Island appears to have resulted in several isolated or disjunct species, of Miocene–Pliocene origin, in mountainous regions (Bell and Patterson 2008; Patterson and Bell 2009; Chapple et al. 2011; Nielsen et al. 2011).

5.3.8 Fiordland

Fiordland is another centre of endemism, with four of the six species known from Fiordland proper endemic to that region and the other two (*M. cryptozoicus* and *O. judgei*) extending only slightly east to the Takitimu Range. Other species, such as *N. gemmeus, W.* 'Otago/Southland large', *O.* aff. *polychroma* clade 5, *O. chloronoton* clade 3c and *O. repens* or *O. toka*, are found in the eastern valleys and foothills, but not in the Fiordland ranges proper.

5.3.9 Stewart Island

Despite having been connected to mainland South Island by continuous dry land during the last glacial maximum, Stewart Island has an endemic genus (*Tukutuku*) and a surprisingly high number of endemic species (*M. nebulosus, O. notosaurus, O. stenotis*) or quite deeply divergent intraspecific clades (*O. chloronoton* clade 3d). The boundary for the Stewart Island fauna falls between Stewart Island and the islands of central Foveaux Strait such as the Ruapuke Group Centre and Pig; these islands have a mainland Southland fauna including species such as *Woodworthia* 'Otago/Southland large', *O. inconspicuum* and the mainland Southland clade of *O. chloronoton*, which are absent from Stewart Island. Only *O. polychroma* and *N. gemmeus* appear to reflect very recent colonisation from or gene flow with the South Island and span this boundary. Notably, these are the same two species that span the Waitaki Valley.

5.4 Updated Biogeographic Patterns for New Zealand Lizards

The last comprehensive attempt to categorise the distributional and biogeographic patterns of New Zealand lizards was made by Towns et al. (1985). However, at the time, there were only 38 species of lizards (22 skinks, 16 geckos) recognised in New Zealand (Towns et al. 1985). The extensive taxonomic activity over the past three decades, characterised by the splitting of several widespread species into multiple taxa and the discovery of numerous new taxa (Chapple and Ritchie 2013; reviewed in Hitchmough et al. 2016a), has increased the size of the New Zealand lizard fauna ~2.7-fold (Hitchmough et al. 2016b) and led to the existing biogeographic categories becoming seriously out-of-date. Whilst there have been several detailed investigations of the biogeography of New Zealand lizards over the past decade (Jewell 2008; Chapple et al. 2009; Nielsen et al. 2011; Di Virgilio et al. 2014; Pepper et al. In Press), none have proposed an updated list of biogeographic categories for the fauna.

Here we assign the 104 currently recognised extant New Zealand lizard species (61 skinks, 43 geckos) to one of 22 different biogeographic categories (Table 5.1). As with Towns et al.'s (1985) categories, our categories are based on the geographic extent of each species, whether they are endemic to a particular region or exhibit a relictual distribution (e.g. due to introduced mammals or human settlement of New Zealand; Chapple et al. 2008a; see Towns et al. 2016). Although we used Towns et al.'s (1985) categories as a basis for ours, adjustment and expansion of these were required for two key reasons. First, the splitting of previously widespread (composite) species into multiple taxa has necessitated the development of additional categories (as an extreme example, *L. nigriplantare maccanni* is now recognised as 19 distinct species; Chapple 2016). As these new taxa generally do not have overlapping geographic distributions and are often restricted to specific regions of the country, the new categories have been designed to reflect this (e.g. Otago endemic, West Coast endemic; Table 5.1). Indeed, many biogeographic breaks in the South Island correspond to provincial boundaries (Figs. 5.3 and 5.4). Second, most newly discovered species/taxa (see Hitchmough et al. 2016a) are only known from a single locality or restricted region, generally mountainous or remote areas of the South Island. Additional categories have been developed to accommodate these species (Table 5.1).

These changes have substantially decreased the number of widely distributed species recognised in New Zealand (12 in Towns et al. 1985 vs 6 in the present study) and dramatically increased the number of island endemics in the North Island and regional endemics within the South Island (see Table 5.1).

5.5 Conclusions

The foundations have been laid for a golden age of New Zealand lizard biogeography. Increasing field surveys, coupled with the continued development of effective sampling techniques (reviewed in Lettink and Hare 2016), have greatly enhanced our knowledge of the distribution of skinks and geckos in New Zealand. This distributional information maintained in a constantly updated, and publicly accessible, online database (Department of Conservation Atlas of the Amphibians and Reptiles of New Zealand; http://www.doc.govt.nz/our-work/reptiles-and-frogs-distribution/atlas/). Importantly, intensive taxonomic work, incorporating molecular studies, has been conducted over the past decade (and is still ongoing), providing enhanced resolution of the true lizard diversity in New Zealand and aiding to delineate species boundaries (reviewed in Hitchmough et al. 2016a). This, for the first time, has provided the essential framework with which to consider the biogeographic patterns evident in the fauna and investigate the processes that have created them. Whilst local extinctions and range contractions, as a result of introduced mammals and human settlement, have been observed, our understanding of prehuman distributions (Worthy and Holdaway 2002; Chapple et al. 2008a), fossil and subfossil evidence has assisted us in reconstructing the previous distributions of several lizard species (Worthy 2016).

Acknowledgements We thank C. Daugherty, and P. Ritchie for advice and assistance during this project. B. Kappers provided access to the New Zealand Department of Conservation's BioWeb Herpetofauna database. DGC was funded by a postdoctoral fellowship from the Allan Wilson Centre for Molecular Ecology and Evolution.

References

Anderson MG, Ferree CE (2010) Conserving the stage: climate change and the geophysical underpinnings of species diversity. PLoS One 5:e11554

Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford

Bauer AM (1990) Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). Bonn Zool Monogr 30:1–218

Bell TP, Patterson GB (2008) A rare alpine skink *Oligosoma pikitanga* n. sp. (Reptilia: Scincidae) from Llawrenny Peaks, Fiordland, New Zealand. Zootaxa 1882:57–68

Berry O, Gleeson DM (2005) Distinguishing historical fragmentation from a recent population decline-shrinking or pre-shrunk skink from New Zealand? Biol Conserv 123:197–210

Bull PC, Whitaker AH (1975) The amphibians, reptiles, birds and mammals. In: Kuschel G (ed) Biogeography and ecology in New Zealand. Dr W. Junk, The Hague, pp 231–276

Campbell HJ, Hutching G (2007) In search of ancient New Zealand. Penguin, Auckland

Carter RM (2005) A New Zealand climatic template back to c. 3.9 Ma: ODP Site 1119, Canterbury Bight, south-west Pacific Ocean, and its relationship to onland successions. J R Soc N Z 35:9–42

Chamberlain CP, Poage MA, Craw D, Reynolds RC (1999) Topographic development of the Southern Alps recorded by the isotopic composition of authigenic clay minerals, South Island, New Zealand. Chem Geol (including Isotope Geoscience) 155:279–294

Chambers GK, Boon WM, Buckley TR, Hitchmough RA (2001) Using molecular methods to understand the Gondwanan affinities of the New Zealand biota. Aust J Bot 49:377–387

Chapple DG (2016) Synthesizing our current knowledge of New Zealand lizards. Chap. 1. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Patterson GB (2007) A new skink species (*Oligosoma taumakae* sp. nov.; Reptilia: Scincidae) from the Open Bay Islands, New Zealand. N Z J Zool 34:347–357

Chapple DG, Ritchie PA (2013) A retrospective approach to testing the DNA barcoding method. PLoS One 8:e77882

Chapple DG, Daugherty CH, Ritchie PA (2008a) Comparative phylogeography reveals pre-decline population structure of New Zealand *Cyclodina* (Reptilia: Scincidae) species. Biol J Linn Soc 95:388–408

Chapple DG, Patterson GB, Bell T, Daugherty CH (2008b) Taxonomic revision of the New Zealand Copper Skink (*Cyclodina aenea*; Squamata: Scincidae) species complex, with description of two new species. J Herpetol 42:437–452

Chapple DG, Patterson GB, Gleeson DM, Daugherty CH, Ritchie PA (2008c) Taxonomic revision of the marbled skink (*Cyclodina oliveri*, Reptilia: Scincidae) species complex, with a description of a new species. N Z J Zool 35:129–146

Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification and systematics of the New Zealand skink fauna (Reptilia: Scincidae). Mol Phylogenet Evol 52:470–487

Chapple DG, Bell T, Chapple SNJ, Miller KA, Daugherty CH, Patterson GB (2011) Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma inconspicuum*; Reptilia: Scincidae) species complex. Zootaxa 2782:1–33

Chapple DG, Birkett A, Miller KA, Daugherty CH, Gleeson DM (2012) Phylogeography of the endangered Otago skink, *Oligosoma otagense*: population structure, hybridisation and genetic diversity in captive populations. PLoS One 7:e34599

Clusella-Trullas S, Blackburn TM, Chown SL (2011) Climate predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. Am Nat 177:738–751

Cooper A, Cooper RA (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. Proc R Soc Lond B 261:293–302

Cooper RA, Millener PR (1993) The New Zealand biota: historical background and new research. Trends Ecol Evol 8:429–433

Coyne JA, Orr HA (2004) Speciation. Sinauer Associates, Sunderland, MA

Craw R (1989) New Zealand biogeography: a panbiogeography approach. N Z J Zool 16:527–547

Cree A (2014) Tuatara: biology and conservation of a venerable survivor. Canterbury University Press, Christchurch

Daugherty CH, Gibbs GW, Hitchmough RA (1993) Mega-island or micro-continent? New Zealand and its fauna. Trends Ecol Evol 8:437–442

Daugherty CH, Patterson GB, Hitchmough RA (1994) Taxonomic and conservation review of the New Zealand herpetofauna. N Z J Zool 21:317–323

Di Virgilio G, Laffan SW, Ebach MC, Chapple DG (2014) Spatial variation in the climatic predictors of species composition turnover and endemism. Ecol Evol 4:3264–3278

Gage M (1980) Legends in the rocks: an outline of New Zealand geology. Whitcoulls, Christchurch

Gibbs G (2006) Ghosts of Gondwana. The history of life in New Zealand. Craig Potton, Nelson

Goldberg J, Trewick SA, Paterson AM (2008) Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. Philos Trans R Soc Lond B 363:3319–3334

Greaves SNJ, Chapple DG, Gleeson DM, Daugherty CH, Ritchie PA (2007) Phylogeography of the spotted skink (*Oligosoma lineoocellatum*) and green skink (*O. chloronoton*) species complex (Lacertilia: Scincidae) in New Zealand reveals pre-Pleistocene divergence. Mol Phylogenet Evol 45:729–739

Greaves SNJ, Chapple DG, Daugherty CH, Gleeson DM, Ritchie PA (2008) Genetic divergences pre-date Pleistocene glacial cycles in the New Zealand speckled skink, *Oligosoma infrapunctatum*. J Biogeogr 35:853–864

Hardy GS (1977) The New Zealand Scincidae (Reptilia: Lacertilia); a taxonomic and zoogeographic study. N Z J Zool 4:221–325

Hare KM, Daugherty CH, Chapple DG (2008) Comparative phylogeography of three skink species (*Oligosoma moco*, *O. smithi* and *O. suteri*; Reptilia: Scincidae) in northeastern New Zealand. Mol Phylogenet Evol 46:303–315

Hayward BW (1986) Origin of the offshore islands of northern New Zealand and their landform development. The offshore islands of northern New Zealand New Zealand Department of Lands and Survey Information Series 16:129–138

Hayward BW (1991) Geology and geomorphology of the Poor Knights Islands, northern New Zealand. Tane 33:23–37

Hickson RE, Slack KE, Lockhart P (2000) Phylogeny recapitulates geography, or why New Zealand has so many species of skinks. Biol J Linn Soc 70:415–433

Hitchmough RA (1997) A systematic review of the New Zealand Gekkonidae. PhD, Victoria University of Wellington, Wellington

Hitchmough RA, Patterson GB, Chapple DG (2016a) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hitchmough R, Barr B, Monks J, Lettink M, Reardon J, Tocher M, van Winkel D, Rolfe J (2016b) Conservation status of New Zealand reptiles, 2015. New Zealand threat classification series. Department of Conservation, Wellington

Hugall AF, Foster R, Lee MSY (2007) Calibration choice, rate smoothing, and the pattern of tetrapod diversification according to long nuclear gene RAG-1. Syst Biol 56:543–563

Jewell T (2007) Fiordland’s lost world. Forest Bird 324:20–21

Jewell T (2008) A photographic guide to reptiles and amphibians of New Zealand. New Holland, Auckland

Jewell T, Tocher M (2005) Skink bomb. N Z Geogr 74:23–25

Kearney M, Porter WP (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species’ ranges. Ecol Lett 12:334–350

King PR (2000) Tectonic reconstructions of New Zealand: 40 Ma to the present. N Z J Geol Geophys 43:611–638

Kluge AG (1967) Higher taxonomic categories of Gekkonid lizards and their evolution. Bull Am Mus Nat Hist 135

Landis CA, Campbell HJ, Begg JG, Mildenhall DC, Paterson AM, Trewick SA (2008) The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. Geol Mag 145:173–197

Lee DE, Lee WG, Mortimer N (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeography and climate. Aust J Bot 49:341–356

Lee MSY, Hutchinson MA, Worthy TH, Archer M, Tennyson AJD, Worthy JP, Scofield RP (2009) Miocene skinks and geckos reveal long-term conservatism of New Zealand’s lizard fauna. Biol Lett 5:833–837

Lettink M, Hare KM (2016) Sampling techniques for New Zealand lizards. Chap. 10. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Lewis KB, Carter L, Davey FJ (1994) The opening of Cook Strait: interglacial tidal scour and aligning basins at a subduction to transform plate edge. Mar Geol 116:293–312

Liggins L, Chapple DG, Daugherty CH, Ritchie PA (2008a) A SINE of restricted gene flow across the Alpine Fault: phylogeography of the New Zealand common skink (*Oligosoma nigriplantare polychroma*). Mol Ecol 17:3668–3683

Liggins L, Chapple DG, Daugherty CH, Ritchie PA (2008b) Origin and post-colonization evolution of the Chatham Islands skink (*Oligosoma nigriplantare nigriplantare*). Mol Ecol 17:3290–3305

Markgraf V, McGlone M, Hope G (1995) Neogene paleoenvironmental and paleoclimatic change in southern temperate ecosystems- a southern perspective. Trends Ecol Evol 10:143–147

McCann C (1955) The lizards of New Zealand. Gekkonidae and Scincidae. Dominion Mus Bull 17

McCann C (1956) The distribution of New Zealand reptiles. Proc N Z Ecol Soc 4:15–16

Miller KA, Chapple DG, Towns DR, Ritchie PA, Nelson NJ (2009) Assessing genetic diversity for conservation management: a case study of a threatened reptile. Anim Conserv 12:163–171

Morgan-Richards M, Rheyda Hinlo M, Smuts-Kennedy C, Innes J, Ji W, Barry M, Brunton D, Hitchmough RA (2016) Identification of a rare gecko from North Island New Zealand, and genetic assessment of its probable origin: a novel mainland conservation priority? J Herpetol 50:77–86

Mortimer N (2004) New Zealand's geological foundations. Gondwanan Res 7:261–272

Neall VE, Trewick SA (2008) The age and origin of the Pacific islands: a geological overview. Philos Trans R Soc Lond B 363:3293–3308

Nelson NJ, Hitchmough RA, Monks JM (2015) New Zealand reptiles and their conservation. In: Stow A, Maclean N, Holwell GI (eds) Austral Ark: the state of wildlife in Australia and New Zealand. University of Cambridge Press, Cambridge, pp 382–404

Nelson-Tunley M, Morgan-Richards M, Trewick SA (2016) Genetic diversity and gene flow in a rare New Zealand skink despite fragmented habitat in a volcanic landscape. Biol J Linn Soc. doi:10.1111/bij.12807

Newnham RM, Lowe DJ, Willaims PW (1999) Quaternary environmental change in New Zealand: a review. Prog Phys Geogr 23:567–610

Nielsen SV, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol 59:1–22

O'Neill SB, Chapple DG, Daugherty CH, Ritchie PA (2008) Phylogeography of two New Zealand lizards: McCann's skink (*Oligosoma maccanni*) and the brown skink (*O. zelandicum*). Mol Phylogenet Evol 48:1168–1177

Patterson GB, Bell TP (2009) The barrier skink *Oligosoma judgei* n. sp. (Reptilia: Scincidae) from the Darran and Takitimu Mountains, South Island, New Zealand. Zootaxa 2271:43–56

Patterson GB, Hitchmough RA, Chapple DG (2013) Taxonomic revision of the ornate skink (*Oligosoma ornatum*; Reptilia: Scincidae) species complex from northern New Zealand. Zootaxa 3736:54–68

Rest JS, Ast JC, Austin CC, Waddell PJ, Tibbetts EA, Hay JM, Mindell DP (2003) Molecular systematics of primary reptilian lineages and the tuatara mitochondrial genome. Mol Phylogenet Evol 29:289–297

Robb J (1973) Reptiles and amphibia. In: Williams GR (ed) The natural history of New Zealand - an ecological survey. A.H. and A.W. Reed, Wellington, pp 285–303

Robb J (1980) New Zealand amphibians and reptiles in colour. Collins, Auckland

Roelants K, Bossuyt F (2005) Archaeobatrachian paraphyly and Pangean diversification of crown group frogs. Syst Biol 54:111–126

Rogers GM (1989) The nature of the lower North Island floristic gap. N Z J Bot 27:221–241

Sharma PP, Wheeler WC (2013) Revenant clades in historical biogeography: the geology of New Zealand predisposes endemic clades to root age shifts. J Biogeogr 40:1609–1618

Smith SA, Sadlier RA, Bauer AM, Austin CC, Jackman T (2007) Molecular phylogeny for the scincid lizards of New Caledonia and adjacent areas: evidence for a single origin of the endemic skinks of Tasmantis. Mol Phylogenet Evol 43:1151–1166

Stevens G, McGlone M, McCulloch B (1995) Prehistoric New Zealand. Reed Books, Auckland

Suggate RP (1982) The geological perspective. In: Soons JM, Selby MJ (eds) Landforms of New Zealand. Longman Paul, Auckland, pp 1–13

Suggate RP, Stevens GR, Te Punga MT (1978) The geology of New Zealand. Government Printer, Wellington

Tingley R, Hitchmough RA, Chapple DG (2013) Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol Conserv 165:62–68

Towns DR (1974) Zoogeography and the New Zealand Scincidae. J R Soc N Z 4:216–226

Towns DR, Daugherty CH, Newman DG (1985) An overview of the ecological biogeography of the New Zealand lizards (Gekkonidae, Scincidae). In: Grigg G, Shine R, Ehmann H (eds) Biology of Australasian frogs and reptiles. Surrey Beatty and Sons/Royal Zoological Society of New South Wales, Chipping Norton/Sydney, pp 107–115

Towns DR, Hitchmough RA, Perrott J (2016) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? Chap. 11. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Trewick SA, Bland KJ (2012) Fire and slice: palaeogeography for biogeography at New Zealand's North Island/South Island juncture. J R Soc N Z 42:153–183

Trewick SA, Paterson AM, Campbell HJ (2007) Hello New Zealand. J Biogeogr 34:1–6

Wallis GP, Trewick SA (2009) New Zealand phylogeography: evolution on a small continent. Mol Ecol 18:3548–3580

Wardle P (1991) Vegetation of New Zealand. Cambridge University Press, Cambridge

Wardle P, Harris W, Buxton RP (1988) Effects of glacial climates on floristic distribution in New Zealand 2. The role of long-distance hybridisation in disjunct distributions. N Z J Bot 26: 557–564

Waters JM, Craw D (2006) Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. Syst Biol 55:351–356

Worthy TH (2016) A review of the fossil record of New Zealand lizards. Chap. 3. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Worthy TH, Holdaway RN (2002) The lost world of the Moa. Prehistoric life of New Zealand. Indiana University Press, Bloomington, IN

Worthy TH, Hand SJ, Archer M, Tennyson AD (2006) The St Bathans Fauna- first insight into Neogene terrestrial vertebrate faunas in New Zealand. 'Geology and Genes' III Geological Society of New Zealand Miscellaneous Publication 121:35–36

Chapter 6
The Ecology of New Zealand's Lizards

Kelly M. Hare, David G. Chapple, David R. Towns, and Dylan van Winkel

Abstract The current distribution of New Zealand lizards has been influenced by past geological events, habitat destruction and introduced predators. Perhaps as a reflection of long isolation, and at least 20 million years of climatic and geological change, the proportion of lizard species that are habitat generalists is relatively low, and high levels of sympatry exist in many environments. Variable strategies in resource partitioning may enable the high sympatry among lizard species, enabling division of resources spatially, temporally and/or trophically. However, overlap in resource use exists, such as honeydew sources, indicating potential competition among and within species. Compared to lizards elsewhere, the New Zealand lizard fauna has some unusual traits, with many species that reside in relatively cool environments, including some that appear to be alpine specialists, some skinks being active at night and *Naultinus* geckos being day active (geckos are globally dominated by nocturnal species). The lizards of New Zealand are highly opportunistic, responding to fluctuating abundance and availability of dietary items throughout the year. Both taxa feed primarily on arthropods, with plant-derived material, other reptiles and carrion also present in the diet; skinks also eat other invertebrates. Both the skinks and geckos of New Zealand disperse seeds and are probably pollinators for some plants. Some New Zealand lizards form aggregations and/or family groupings, and parental care may also be present. Some species use habitat differently in the presence of predators, which include native and introduced birds and invertebrates, native reptiles and introduced amphibians and reptiles.

K.M. Hare
Centre for Biodiversity and Restoration Ecology, Victoria University of Wellington, Wellington, New Zealand

D.G. Chapple (✉)
School of Biological Sciences, Monash University, Clayton, VIC 3800, Australia
e-mail: david.chapple@monash.edu

D.R. Towns
Department of Conservation, Auckland New Zealand and Institute for Applied Ecology New Zealand, Auckland University of Technology, Auckland, New Zealand

D. van Winkel
Bioresearches Group Ltd, Auckland, New Zealand

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_6

Keywords Behaviour • Diet • Gecko • Habitat use • Mating behaviour • Pollination • Predation • Seed dispersal • Skink

6.1 Introduction

Ecology is an interdisciplinary field that includes all branches of biology, plus elements of geography and the earth sciences, but focusses in particular on the interactions among organisms and their environment (Molles 2013). Ecological data, distribution, habitat use, trophic interactions and behavioural responses, are useful for most disciplines in the biological sciences, but in particular are required for effective conservation management. With at least 61 extant species of skinks (Scincidae) and 43 species of gecko (Diplodactylidae), New Zealand has the most diverse lizard assemblage of any temperate archipelago (here species refers to both described and undescribed entities; Daugherty et al. 1990; Hitchmough et al. 2016a, b). Lizards have been present in New Zealand since the Eocene-Oligocene (geckos) or Miocene (skinks) (Worthy 2016; Chapple and Hitchmough 2016), living in an environment that not only had a different vegetation structure, but was completely free of introduced mammalian predators and terrestrial snakes (Chapple and Hitchmough 2016). These historical factors, coupled with many species showing strategies such as late maturity and low annual reproductive output (Cree and Hare 2016; Cree 1994), make New Zealand's lizards particularly vulnerable to novel external influences. Most lizards of New Zealand have undergone large-scale range contractions since human settlement (~1000 ya), through a combination of effects from habitat modification and predation by introduced fauna, especially mammals (Towns et al. 2016). As such, many species require direct conservation management (Tingley et al. 2013), for which knowledge of their ecology is vital.

This chapter examines the ecological characteristics of New Zealand's lizards, including their distribution, habitat use, behaviour and trophic interactions (inter- and intraspecific interactions, diet and predators). We note that many factors important to understanding the ecology of New Zealand's lizards are outlined elsewhere in this volume; here, we may touch on them briefly but will ultimately refer the reader to the other chapters. Our aims in undertaking this review are to: (1) provide a broad overview of several key aspects of lizard ecology in New Zealand, and (2) to indicate any areas that particularly require further investigation. We preferentially use data from wild populations, noting where data are from captive sources. We do not aim to be comprehensive in coverage, instead we point the reader to primary literature and more in-depth studies. However, we do attempt to outline various differences in the ecology of skinks and geckos within a New Zealand context, and compare them with similar species overseas.

6.2 Distribution, Habitat Use, Sympatry and Resource Partitioning

6.2.1 Distribution and Habitat Types Within New Zealand's Islands

New Zealand is a long narrow archipelago of over ~650 islands spanning ~1600 km along a north-northeast axis, with a maximum land width of ~400 km. Altitude ranges from 0 m a.s.l along the extensive coastline of New Zealand (~15000 km) to mountain peaks reaching 3754 m a.s.l (Gibbs 2006; Neall and Trewick 2008). Prior to human settlement (~1000 ya), lizards were found throughout all islands of New Zealand, except the near sub-tropical Kermadec Islands and the Sub-Antarctic Islands (Worthy 2016). Although much reduced in range, species of skinks and geckos are still present throughout the mainland and offshore islands from the Three Kings Islands north of North Island to Rakiura/Stewart Island in the far south; latitudes from 34 to 47°S (Chapple and Hitchmough 2016). Distribution among habitats is similarly broad, with some lizard species from both families found in environments ranging from coastal beaches (0 m a.s.l) to alpine scrub and scree (~2200 m a.s.l) and from forest to regenerating scrub to tussock grasslands. Some species are also present in what might be termed marginal habitats, on offshore rock stacks, in modified agricultural lands and/or in urban settings (e.g. Barwick 1959; Liggins et al. 2008; Reardon et al. 2012). Although a few species (~7 %) could be termed as generalist in their habitat distribution (e.g. present from the coast to subalpine regions; Fig. 6.1a, b), most can be classified into more defined geographic distributions. For example, some *Oligosoma* are only found along the coastal shoreline (e.g. *O. suteri* and *O. acrinasum*; Towns 1975; Thomas 1985) and some only in alpine regions (e.g. *Mokopirirakau kahutarae*, Whitaker 1984). Interestingly, no geckos have been observed to be strictly coastal, whereas five species of skinks are classified as coastal dwellers, inhabiting the shoreline and sometimes entering coastal scrub (Towns et al. 1985). As more data are obtained on the distributions of species, it is likely that habitat classifications will alter and that more refined habitat classifications will be possible.

6.2.2 Sympatry and Resource Partitioning

Environmental resources are generally partitioned in three main ways, temporally, spatially and trophically, that is, by time of activity, spaces used and/or foods eaten (Whitaker 1968; Towns et al. 1985). Resource partitioning reduces competition and is probably how many species can coexist (e.g. Towns et al. 1985; Box 6.1). However, when only one potential resource partitioning character is used, character displacement among species may not be found. For example, Montoya and Burns (2007) concluded that where little support was found for character displacement

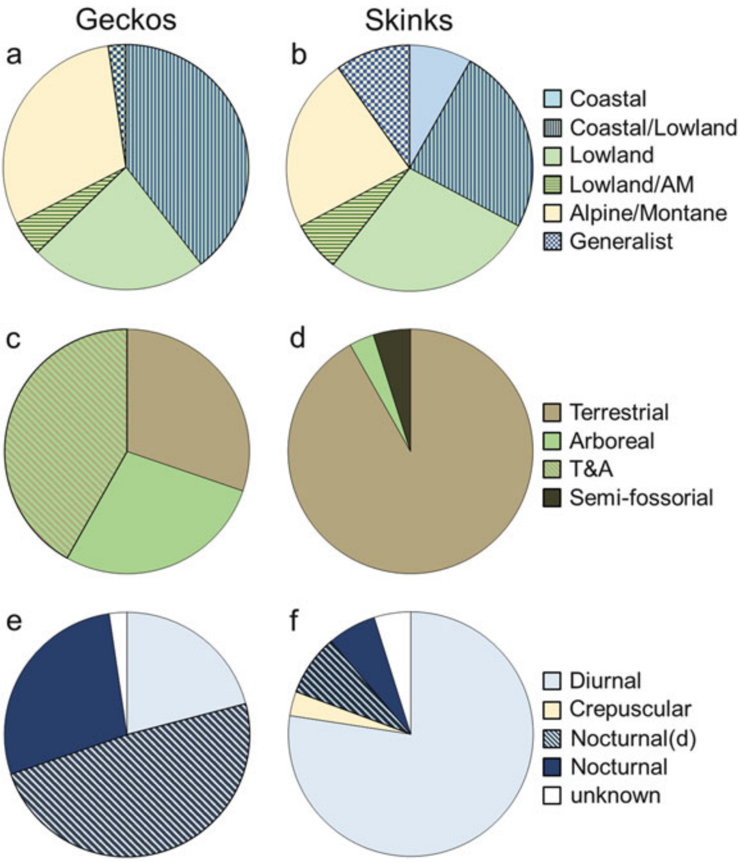
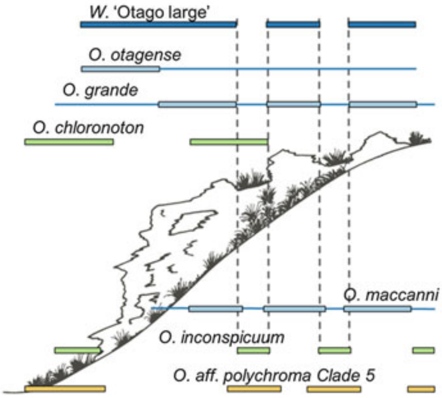


Fig. 6.1 Habitat use and activity times of endemic gecko ($N = 43$) and skink species ($N = 61$) from New Zealand. *Top row*. Biogeographic affinity for: (**a**) geckos and (**b**) skinks. Coastal = 0–50 m a.s.l; lowland = 50–500 m a.s.l; alpine/montane (AM) ≥ 500 m; generalist = present from coast to alpine regions. *Middle row*. Habitat use for: (**c**) geckos and (**d**) skinks. Terrestrial = found on ground; arboreal = found in trees/scrub (may use terrestrial retreats); T&A = uses both terrestrial and arboreal structures; semi-fossorial = terrestrial species that uses burrows and leaf litter. *Bottom row*. Main activity/foraging times for: (**e**) geckos and (**f**) skinks. Diurnal = diurnally foraging; crepuscular = dawn and dusk foraging (NB both crepuscular skink species have also been seen basking by day); nocturnal (d) = nocturnally foraging species seen basking by day; nocturnal = nocturnally foraging. Data and groupings are based on Tingley et al. (2013); with some additional data since 2013 available from the corresponding author on request. *Note*: these charts show general trends and should not be used as absolute values (see text for more explanation)

(due to body size and diet preference) on some islands, other factors, such as interspecific differences in habitat selection and/or diurnal activity patterns, may interact with differences in prey size selection to promote coexistence among *Oligosoma* skinks.

Box 6.1 Resource partitioning

The lizards of New Zealand have a high level of sympatric species diversity, most likely through resource partitioning at temporal, spatial and trophic scales (i.e. time of activity, spaces used, and/or foods eaten). One surprisingly diverse lizard fauna is among the fractured schist rock outcrops (tors) and steep gullies of the Otago high country (see diagram and references cited within), where seven lizard species may be found on or near each tor.



Habitat use of lizards in subalpine tussock grasslands of Central Otago. Habitats used often are shown by solid bars, with solid connecting lines indicating less-used habitats. Blue = saxicolous/ rock dwelling; Green = herbs and shrubs; Gold = tussock grasslands. Figure modified with permission from Towns et al. 1985 © Royal Society of New South Wales, updated using Patterson and Daugherty 1990, Berry et al. 2005, R. Mules pers comm.

The only nocturnally foraging species is the gecko *W.* 'Otago large' which by day may form large aggregations under rock plates and in rock crevices. The largest skink species, *Oligosoma otagense,* most commonly uses fractured sunny rock faces on bluffs, and the smaller *O. grande* are more common on exposed and isolated tors. Similar in size to *O. grande* are *O. chloronoton*, which may occasionally bask, but are most active on large tors in the cooler months of spring moving in the hot summer months to cooler vegetated gullies. Of the three smaller skinks, *O. maccanni* is commonly found under rocks near the base of tors, and may use herbs and shrubs, the rarely seen *O. inconspicuum* is usually associated with vegetated gullies and damper areas, preferring herbs and shrubs, and *O.* aff. *Polychroma* Clade 5 occasionally bask on tors, but more commonly inhabit grasslands. Dietary separation may exist among the skinks which vary in size, and also alter food preference seasonally (see section 6.3). Further north, even more diverse, but spatially constrained lizard assemblages exist on some islands (Towns et al. 1985). For example, on Middle Island, Mercury Island Group, 10 lizard species are segregated spatially as terrestrial, arboreal, or burrow-inhabiting, as well as by time of activity and size.

Box 6.1 Resource partitioning

Despite the varied habitat distribution among New Zealand lizards, sympatric species diversity is unusually high for a temperate region (Towns and Daugherty 1994; Chapple et al. 2011). Local assemblages may comprise large numbers of lizard species (Towns and Daugherty 1994), and one example is from native tussock grasslands of the southeastern South Island, which provides habitat for six skink and one gecko species (Towns et al. 1985; Whitaker et al. 2002; Box 6.1). However, higher diversities are present in some northeastern offshore islands. For example, 13 ha Middle Island (Mercury Islands Group) has three species of gecko and seven species of skink (Towns and Daugherty 1994). These high species diversities are probably possible through the partitioning of environmental resources, but comprehensive niche studies including temporal, spatial and trophic interactions are rare (but see Towns 1975; Towns et al. 1985).

Prior to human arrival, natural densities of lizards were probably very high. For example, at Turakirae Head, Wellington, densities of *W. maculata* populations in the early 1980s were estimated conservatively to be ~4000 per ha (Whitaker 1982), *Toropuku stephensi* at 600 per ha in vinelands on Stephens Island (Hare and Cree 2005) and *O. lineoocellatum* between 1000 and 8000 per ha, depending on location (references within Towns et al. 2002). To facilitate such high densities, often with different species coexisting in finite space, either environmental resources are partitioned or intra- and interspecific competition is very high.

6.2.3 Habitat Use and Movement by New Zealand's Lizards

Studies of lizard communities often categorise lizards by whether they use elevated perches or not, with perches including arboreal and saxicolous (rock dwelling) microhabitats (Vitt et al. 2003). Although we acknowledge that saxicolous habitats may be elevated in some cases (e.g. isolated rock outcrops; tors at Macraes Flat, Otago; Fig. 6.2a), in terms of the New Zealand environment, saxicolous habitats include rock tors, rocky scree, rocky cliffs and/or boulder banks; not all of which are elevated (Fig. 6.2a, b, e). Thus, here we have continued to use the broader classification outlined in Tingley et al. (2013): terrestrial (use the ground, including rocks) and arboreal (use tree/scrub vegetation). In addition, we add semi-fossorial as a category to indicate terrestrial species that primarily use burrows and/or deep leaf litter (Fig. 6.1 d).

In general, New Zealand geckos are classified as arboreal, terrestrial or 'both' (i.e. use both environments while foraging); all *Naultinus* geckos and two *Mokopirirakau* spp. are arboreal (some use refuges on the ground, D van Winkel unpublished data), with the remaining geckos classified as terrestrial (30 %). In contrast, the skinks are generally recorded as terrestrial (92 %; Fig. 6.1d), despite observations of some terrestrial species foraging within scrub and/or trees. For example, the primarily terrestrial *O. fallai* has been observed foraging in trees up to 3 m off the ground (Parrish and Gill 2003), and the saxicolous *O. otagense* is often observed foraging for berries in short scrub (Fig. 6.3c). A more in-depth examination of intra- and interspecific variation in habitat use is warranted, especially for skinks. As additional ecological studies are completed on New Zealand's lizard species, it is likely that revision and reclassification of habitat use categories will be needed.

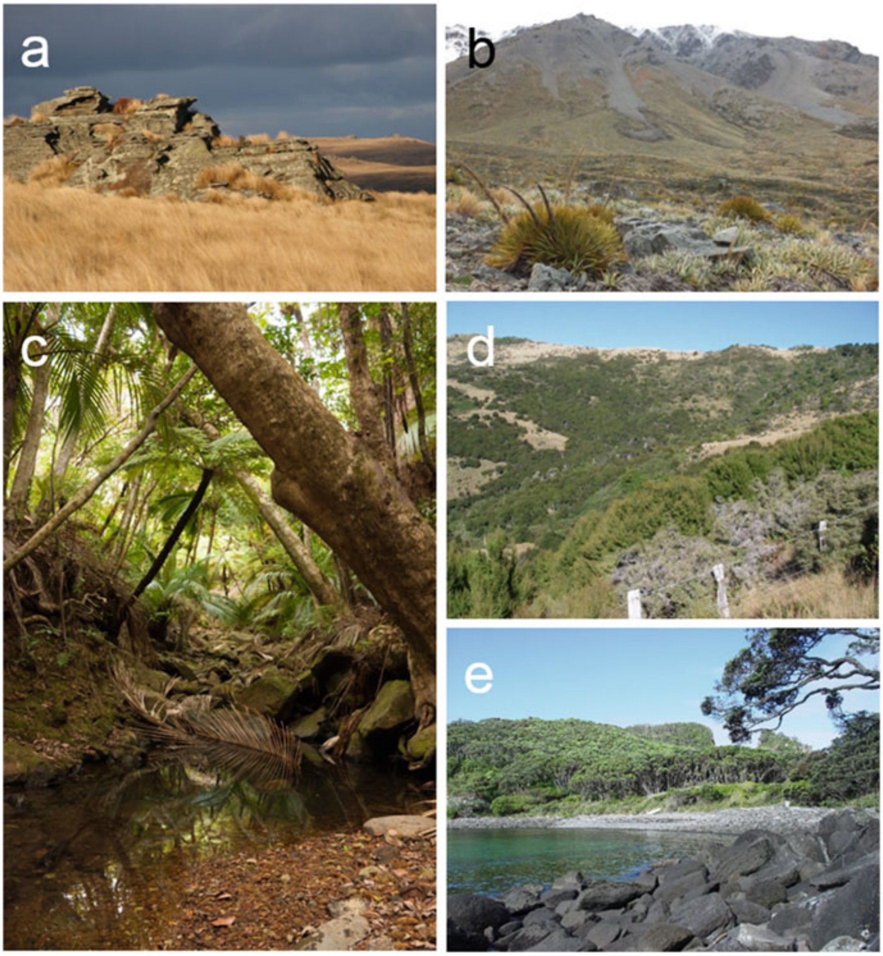


Fig. 6.2 Examples of habitats used by endemic lizards in New Zealand. (**a**) Modified (periodically burnt for agriculture) tussock grassland at Macraes Flat, Otago (Photo: © Grand and Otago Skink Recovery Programme, New Zealand Department of Conservation). (**b**) Mt Somers Range in alpine/montane area around 1000 m a.s.l (photo: © Marieke Lettink). (**c**) Forest habitat on Great Barrier Island (Photo: © Dylan van Winkel). (**d**) Regenerating shrubland/forest in lowland Banks Peninsula (photo: © Marieke Lettink). (**e**) Coastal forest and boulder beach on Korapuki Island, Mercury Island Group (photo: © David Towns)

Knowledge of microhabitat use, including habitat preferences, movement patterns and the use of retreat sites, provides ecological information helpful in optimising sampling techniques (Lettink and Hare 2016) and accurately evaluating threat status and population trends for conservation (Tingley et al. 2013). Despite the number of lizard species, detailed studies of habitat use by New Zealand lizards are rare, but some excellent examples exist (e.g. Barwick 1959; Towns 1975; Hitchmough 1979; Neilson et al. 2006). This deficit in data is probably due to the

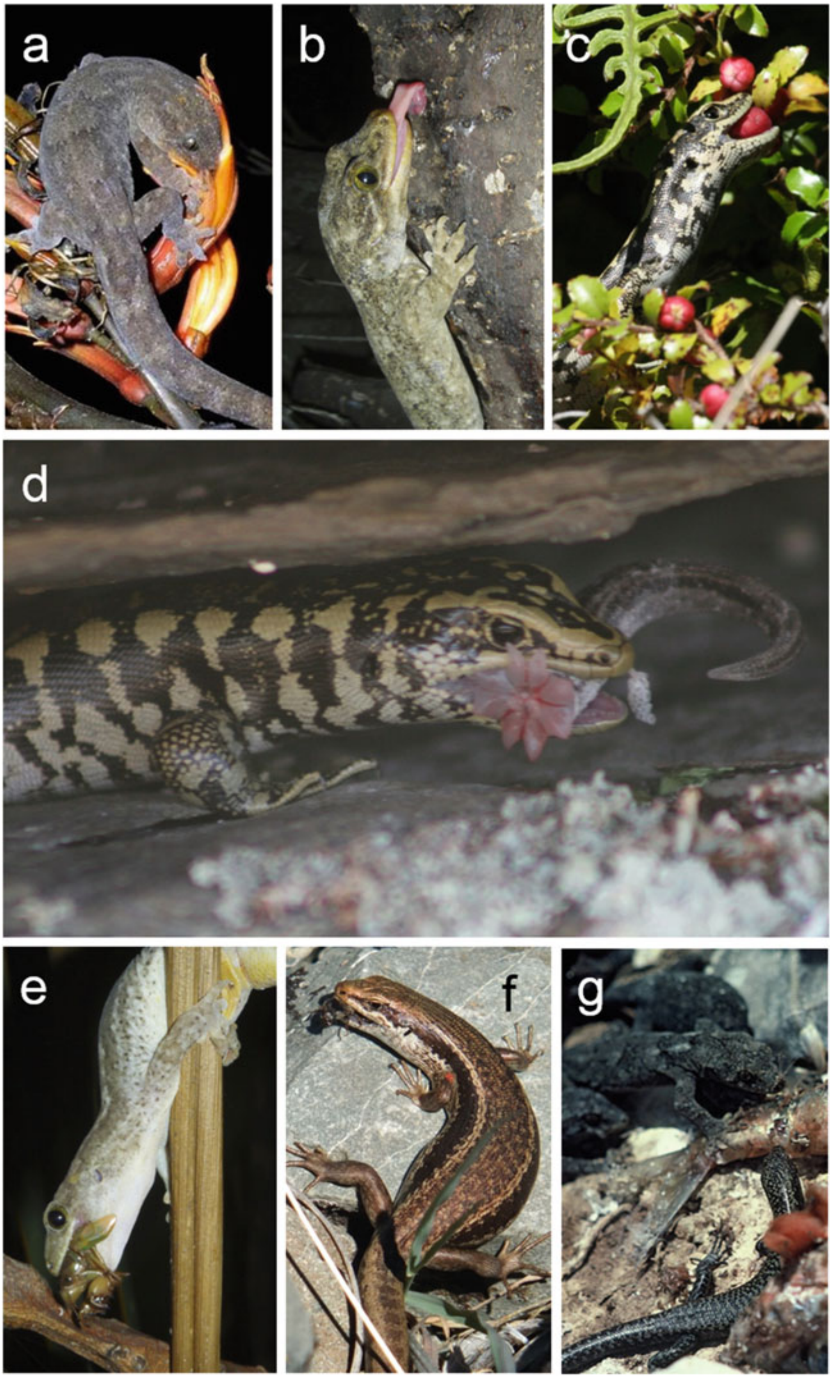


Fig. 6.3 Diet and foraging behaviour of endemic lizards of New Zealand. (**a**) *Woodworthia maculata* drinking nectar from a flower of *Phormium* sp.; pollen is visible on the back of the head (Photo: © Kelly Hare). (**b**) *Hoplodactylus duvaucelii* licking honeydew oozing from a

long hours of field-work required, coupled with the often cryptic nature and relatively small body size of native lizards (Hare et al. 2007; Cree and Hare 2016). As new techniques and technologies are developed (e.g. lighter and smaller transmitters, camera stations (see Lettink and Hare 2016) and drones), more detailed studies are likely to be possible.

Habitat structure can influence the movement patterns of lizards (McIntyre and Wiens 1999). Familiarity with the landscape may minimise energy expenditure while searching for resources such as food, retreats and mates and reduce time spent in unsuitable habitat, i.e. aid in predator avoidance (e.g. Hoare et al. 2007). Thus, resident animals often move in a predictable manner due to familiarity with their environment (Plummer and Mills 2000). Movement data and dispersal of New Zealand lizards have been recorded through direct observation (*H. duvaucelii*, Whitaker 1968), recaptures of individuals from evenly spaced pitfall traps and/or artificial covers (e.g. *O. whitakeri*, Towns and Elliott 1996; *W.* cf. *brunnea*, Lettink 2007), using telemetry (e.g. *M.* 'Southern forest' Hoare et al. 2013; *O. grande*, Gebauer 2012; *O. otagense*, Eifler and Eifler 1999a) and/or through genetic (e.g. *O. grande*, Berry et al. 2005) and stable isotope studies (*O. suteri*, Janssen et al. 2015). Additionally, populations of a species may vary in their use of habitat. For example, the obligate coastal skink *O. suteri* appears to vary in habitat use depending on their size (e.g. Towns 1975). Since conventional tracking is not possible for *O. suteri* in their boulder beach habitats, Janssen et al. (2015) compared the ratios of isotopes (^{13}C:^{15}N) of skinks and their prey. Larger skinks (>75 mm SVL) on one island site consumed more terrestrial invertebrates from rank grassland than those <75 mm, which fed mostly on marine species (Janssen et al. 2015). Thus, studies using stable isotopes can add to more conventional habitat-use studies.

Many New Zealand lizards show strong site fidelity, some over extraordinarily long periods of time. Some examples include the following: over an 8-year monitoring study, 92 % of *W. maculata* at Turakirae Head, Wellington, were found within 5 m of previous sightings (Whitaker 1982); one female *H. duvaucelii* from North Brother Island was found within 5 m of its original capture point 29 years later (Thompson et al. 1992); and five of six *O. lineoocellatum* from North Brother Island were within 15 m of their original capture point 5 years later (Hoare et al. 2005). Many other New Zealand lizards have been recorded to have strong

Fig. 6.3 (continued) Myoporum laetum branch (Photo: © Dylan van Winkel). (**c**) The saxicolous skink, *Oligosoma otagense*, plucking fruit after climbing a *Gaultheria antipoda* shrub (Photo: © Riki Mules). (**d**). *Oligosoma otagense* eating the freshly autotomised tail of the gecko *Woodworthia* 'Otago large'; the skink was seen grabbing the tail of the gecko and later consuming it; the autotomized tail is curled in mid-movement (Photo: © Grand and Otago Skink Recovery Programme, New Zealand Department of Conservation). (**e**) *Woodworthia maculata* eating a cicada (Order Arthropoda; Photo: © Dylan van Winkel). (**f**) *Oligosoma longipes* eating a beetle (Order Arthropoda); orange parasitic mites (*Odontacarus* sp.) are visible in the left axilla (Photo: © Marieke Lettink). (**g**) A skink (*Oligosoma smithi*) and three geckos (*Dactylocnemis* 'Poor Knights') eating regurgitated fish from a seabird (Photo: © Rod Morris/rodmorris.co.nz) site fidelity; some examples include: *W. chrysosiretica* (Flannagan 2000), *W.* cf. *brunnea* (Lettink 2007), *T. stephensi* (Hare and Cree 2005), *O. whitakeri* (Southey 1985) and *O. grande* (Coddington and Cree 1997).

A revealing study of habitat use was of the large secretive skink *O. homalonotum* on Great Barrier Island. Transmitters on eight adult skinks showed that while tracked they only moved short distances (mean = 2.8 m), remained within 13 m of forested streams and occupied debris dams, burrows in soil, crevices in trees and the crowns of tree ferns and palms (Neilson et al. 2006). However, *O. homalonotum* may move much larger distances, up to 58 m away from streams (Barr 2009). Of note, capture, including attachment of transmitters, can alter the behaviour of animals and may elicit some large-scale movements (e.g. Germano 2005). Additionally, translocated individuals may behave differently from individuals in source populations. For example, movements and range sizes in translocated *H. duvaucelii* are larger than in resident populations (van Winkel 2008), with adult geckos on Tiritiri Matangi Island and Motuora Islands moving up to 34.3 m per day and having range areas up to six times larger (mean = 1524 m^2) than resident non-translocated populations. This is compared with *H. duvaucelii* on the Poor Knights Islands, which move up to 25 m per night (Whitaker 1968) and *H. duvaucelii* on Ruamahua-Iti Island which may range over 210 m^2 within three nights (Christmas 1995).

Dispersal after translocation is common among animals (Le Gouar et al. 2012) and may be a contributing factor to the historically low success rate of herpetofaunal translocations (Miller et al. 2014). Thus, improving site fidelity of translocated individuals is vital (Germano and Bishop 2008); the technique of penning prior to release may reduce dispersal among translocated individuals, at least in *N. gemmeus* (Knox and Monks 2014). Of interest, some species show strong homing ability, which may also account for some of the large-scale movements recorded post-translocation. For example, over a 9-week period, 54 % of displaced *O. grande* returned to their capture tor, with no difference in homing abilities apparent between age classes and sexes (Stanley 1998). The skinks showed a negative correlation between homing ability, time to home and distance moved, and no individuals homed when moved >100 m (Stanley 1998). Similarly, some *W. maculata* have been observed to return at least 110 m to their capture location over 32 days (Marshall 1983). However, some species show no apparent homing ability (e.g. *W.* cf. *brunnea*; Lettink 2007).

6.3 Diet, Seed Dispersal and Pollination

Animals tend to exploit food resources that offer maximum nutritional or energetic returns relative to time spent foraging (Pyke et al. 1977). Dietary components have been determined by direct observation of individuals, through stomach or scat analyses (e.g. Barwick 1959; Towns 1975), or through stable isotope analyses; the latter of which may be more reflective of diet over long periods (e.g. Janssen et al. 2015). Dietary components have been reported for 40 species of lizards (38 %)

in New Zealand, and most appear to be omnivorous. The main items recorded in the diet of skinks and geckos are arthropods (e.g. Table 6.1), but other organisms are often consumed, including smaller lizards or autotomized tails and carrion of larger vertebrates (Table 6.1). However, no 'other invertebrates' (e.g. molluscs and worms) have yet been recorded in the diet of geckos (Table 6.1). Many lizard species feed on coastal invertebrates and carrion (e.g. Fig. 6.3 g) and must cope with the physiological challenges of high salt content in their food. One species, *O. suteri*, overcomes this problem by secreting sodium (Na) from nasal salt glands (Janssen et al. 2015). Whether other species found near the coast are similarly adapted to salty diets is unknown. Some New Zealand lizards (~60 %) also readily eat sugar sources of fruit, honeydew and nectar (Evans et al. 2015; Wotton et al. 2016; Fig. 6.3a, b, c) and other plant matter (Table 6.1). Consumption of 'other' plant matter is often assumed to be accidental ingestion during prey capture (e.g. Freeman 1997). However, *O. grande* have been observed systematically plucking and consuming the bright yellow petals of *Hieracium* spp. flowers (Tocher 1998); prior to this observation, petals were assumed to be consumed accidentally.

Internationally, lizard-plant interactions are regarded as rare and less important than bird-plant and insect-plant interactions for both the ecology and evolution of plants (Olesen and Valido 2003, 2004). However, evidence from New Zealand studies suggests that lizards are, or once were, important components of plant reproductive strategies (e.g. Whitaker 1987; Towns and Daugherty 1994; Wotton et al. 2016). To date, the fruits of 23 native plant species have been recorded as being consumed by New Zealand's lizards, with greater numbers of white–blue fruits eaten than red fruits (see Wotton et al. 2016 for review). Additionally, lizards can disperse seeds, which later germinate up to around 20 m from the parent plant, allowing seeds to disperse to safe establishment sites (Wotton et al. 2016). Thus, lizards are important seed dispersers, even at reduced densities on the mainland, and in areas lacking frugivorous birds may be the only dispersers present (Whitaker 1987; Wotton et al. 2016).

Lizards can also be effective pollinators (Traveset and Sáez 1997; NyHagen et al. 2001), and one of the earliest suggestions that lizards are pollinators was based on observations on New Zealand geckos (Whitaker 1987). In one study over two-thirds of geckos (*Dactylocnemis* 'Poor Knights') visiting flowers were observed to carry pollen, with pollen being carried up to at least 50 m from the source plants and for at least 12 h, providing opportunity for cross-pollination (Whitaker 1987). The reported density of gecko visitors on flowers in New Zealand is between 5 and 8 geckos per m^2 (Whitaker 1968, 1987), with up to five geckos observed feeding together on a single inflorescence (Whitaker 1987). Lizard densities reported on flowers in New Zealand are around three times greater than reported in international studies (Eifler 1995). However, coevolution of lizards and plants appears unlikely as, to date, no plants have been recorded as being peculiarly adapted for pollination by lizards (Whitaker 1987); additionally, some studies suggest that lizards play a minor role in the New Zealand pollinator systems (Newstrom and Robertson 2005).

Table 6.1 Items recorded in the diet of New Zealand lizards in the wild

Species	Plant matter				Chordates				Arthropods						Other invertebrates				Sources
	Fruit	Honeydew	Nectar	Other	Bird	Fish	Mammal	Reptile	Arachnida	Chilopoda	Diplopoda	Entognatha	Insecta	Malacostraca	Annelida	Mollusca	Nemotoda	Platyhelminthes	
Skinks																			
Oligosoma acrinasum									●		●		●	●		●			Thomas (1985)
[a]*Oligosoma aeneum*	◊							●	●				●	●	●	●	●		McCann (1955), Porter (1987), and Barwick (1959)
Oligosoma alani	●					●		●	●	●	●	●	●	●		●			Southey (1985)
Oligosoma fallai	●			●	●	●			●	◊	◊	◊	●	●					Parrish and Gill (2003), Whitaker (1968), and McCann (1955)
Oligosoma grande	●			●					●				●						Tocher (2003), Eifler and Eifler (1999a,b), and Tocher (1998); Fig. 6.3b
Oligosoma homalonotum									●				●			●			Towns et al. (2002)
Oligosoma inconspicuum	●							●	●	●	●	●	●	●	●	●		●	Patterson (1985)
Oligosoma infrapunctatum	●												●						Efford et al. (1997) and Duncan (1999)
Oligosoma lineoocellatum	●		●					●	●		●		●	●	●	●			Spencer et al. (1998), Towns et al. (2002), Robb (1980), and Phillpot (2000)
Oligosoma longipes													●						Figure 6.3f
[a]*Oligosoma maccanni*	●			●				●	●	●	●	●	●	●	●	●		●	Freeman (1997), Patterson (1985, 1992)
Oligosoma macgregori									◊	◊	◊		●	◊					Robb (1980)

Oligosoma moco	●		●						◊	◊	◊	◊	●	◊					Whitaker (1968), Wotton et al. (2016), Patterson (1992), and Stephenson (2012a)
Oligosoma nigriplantare						●			◊	◊	◊	◊	●	◊					Fleming (1939) and Robb (1980)
Oligosoma oliveri	●				●	●			●	●	●			●		●			Southey (1985)
Oligosoma ornatum				●					●				●	●	●	●			Porter (1987)
Oligosoma otagense	●							●	●				●						Tocher (2003); Fig. 6.3c
[a]*Oligosoma polychroma*	●								●				●	●	●	●	●		Gill (1976) and Barwick (1959)
[a]*Oligosoma* aff. *polychroma* Clade 5	●							●	●	●	●	●	●	●	●	●	●		Patterson (1985) and Freeman (1997)
Oligosoma smithi	●				●	●			◊	◊	◊	◊	●	◊					Towns (1972), Whitaker (1968) and Towns et al. (2002); Fig. 6.3 g
Oligosoma striatum													○						Melgren (1980)
Oligosoma suteri						●	●	●					●	●		●			Towns (1975); Parrish and Gill (2003) and Stephenson (2012b)
Oligosoma whitakeri	●								●	●	●			●		●			Southey (1985)
Oligosoma waimatense	●			●				●	◊	◊	◊	◊	◊	◊					Whitaker (1985) and Patterson (1997)
Oligosoma zelandicum								●	●			●	●	●		●			Gill (1976)

(continued)

Table 6.1 (continued)

Species	Plant matter				Chordates				Arthropods						Other invertebrates				Sources
	Fruit	Honeydew	Nectar	Other	Bird	Fish	Mammal	Reptile	Arachnida	Chilopoda	Diplopoda	Entognatha	Insecta	Malacostraca	Annelida	Mollusca	Nemotoda	Platyhelminthes	
Geckos																			
Dactylocnemis pacificus	●		●										●						Robb (1980)
[a]*Dactylocnemis* 'Poor Knights'	●		●			●							●						Wotton et al. (2016) and Whitaker (1968); Fig. 6.3 g
Hoplodactylus duvaucelii	●	●	●	●	●			●	●				●						Whitaker (1968), Barwick (1982) and Harper (1983); Fig. 6.3b
Mokopirirakau 'Southern forest'													●						Hoare et al. (2013)
Naultinus elegans													●						Robb (1980)
Naultinus grayii	●												●						Hitchmough (1982) and Wotton et al. (2016)
Naultinus manukanus									◊	◊	◊	◊	○	◊					Robb (1980)
Naultinus stellatus	○												●						Conway and Gaynor (1979) and Robb (1980)
Naultinus tuberculatus													●						Robb (1980)
Toropuku stephensi	●																		Wotton et al. (2016)
Tukutuku rakiurae									○				○	○					Thomas (1981)
[a]*Woodworthia* cf. *brunnea*	●																		Freeman (1994)

Woodworthia chrysosiretica									●				●						Robb (1980)
Woodworthia maculata	●	●	●						●				●						Evans et al. (2015) and Whitaker (1982); Fig. 6.3a
Woodworthia 'Southern Alps'	●																		Wotton et al. (2016)

Data were selected from published sources, theses and reports (in that order, with citations with the most data selected first; i.e. not all citations are listed). Dietary item included as: *filled circle* = lizard directly observed eating item and/or item found in stomach contents and/or in faeces; *unfilled circle* = reported as in diet, but specific item not reported; *diamond* = inferred as in diet. Other plant matter refers to leaves and petals. Birds include carcasses and/or broken eggs. Reptiles may include only the consumption of tails. Fish is either regurgitated from birds and/or carcasses. Mammals refer to consumption of carcasses

[a] Species has been inferred from its geographic location coupled with taxonomy outlined in Hitchmough et al. (2016a)

Reported consumption of sugar sources by skinks is mainly for fruit, with only two skinks recorded as drinking nectar (*O. lineoocellatum* and *O. moco*; Towns et al. 2002; Stephenson 2012a), and none reported to consume honeydew. However, geckos are avid drinkers of nectar. An experiment whereby the volume of nectar (53 % [sugar]) was increased artificially by 40–100 % not only increased the number of geckos visiting flowers, but geckos appeared to select stalks with more male flowers (Eifler 1995); male flowers have higher rates of nectar secretion and higher sugar concentrations than female flowers. Similarly, numbers of geckos increased exponentially as numbers of inflorescences increased indicating that gecko distribution reflects nectar availability (Eifler 1995). However, long-term studies indicate that the diet of New Zealand's lizards probably fluctuates throughout the year, changing opportunistically with season and environmental temperature (e.g. Whitaker 1982; Tocher 2003).

Few studies indicate the sizes of prey items, but those that do tend to show the expected trend for the size of prey consumed to be proportional to the size of the species (e.g. Hitchmough 1979; Whitaker 1982); smaller species tend to eat smaller-sized items. However, lizards will attempt to eat large items too, which can be to their detriment. For example, a skink (*O. oliveri*) was observed choked to death on a scavenged piece of fish (Whitaker 1968). Finally, trends in diet are not always straightforward. For example, some species show sex-biased difference in some studies, but not others, although this may be related to seasonal differences in food availability. For example, in March *O. grande* males tend to attempt to catch large strong-flying insects, and males use a salutatory search pattern (where individuals alternatively move and pause while foraging; Eifler and Eifler 1999b), whereas females eat more frequently and spent more time eating. However, a later study showed no difference in diet among sites, ages classes and sexes, but showed an increase in fruits eaten in May (53 %) compared with November (20 %; Tocher 2003). Thus, food intake and dietary diversity varies considerably among the seasons. Of interest, some species have been recorded eating items that are presumably not present during their purported activity phase. For example, in one study *O. lineoocellatum* consumed more nocturnal (53 %) than diurnal prey items (32 %; Spencer et al. 1998), which suggests either incorrect apportioning of activity period to prey items, or activity at night by these diurnally foraging skinks.

6.4 Activity and Behaviour

6.4.1 Classification and Measurement of Activity Phase of Geckos and Skinks

Squamates are ancestrally diurnal ectotherms, and diurnal activity is more likely to enable them to reach body temperatures necessary for activity and physiological functions (Hare and Cree 2016). Among squamates, only the ancestor of geckos and

Autarchoglossa (skinks, anguimorphs, snakes and relatives) has evolved nocturnality (Vitt et al. 2003). The use of time (temporal niche) varies among lizard species; historically, species have been classified as either diurnal (day active), nocturnal (night active) or crepuscular (active dawn and dusk). More recent studies include a 'both' (nocturnal and diurnal) or 'nocturnally foraging' classification (Pianka and Vitt 2003; Gibson et al. 2015), as a way to show that many lizard species are not constrained by our classifications of activity; and this variability appears to be especially true for New Zealand's lizards. For example, of the 33 nocturnally foraging geckos, 64 % have been observed emerged and basking during the day (e.g. Fig. 6.4b) although no diurnally foraging geckos (all *Naultinus*) have yet been observed active at night (Fig. 6.1e). For the skinks, activity patterns are less well defined. Within the nine species of nocturnally foraging skinks around half have also been observed foraging by day and/or at dawn and dusk (Fig. 6.1f; *O. oliveri*, *O. ornatum*, *O. macgregori*, *O. suteri* and *O. whitakeri*; Robb 1980; Porter 1987; Towns 1999), and one (*O. fallai*) has been reported as both strongly active during the day and night (Parrish and Gill 2003). Additionally, some diurnal skinks have been observed foraging at night (e.g. captive *O. striatum*; Whitaker 1998). Interestingly, all nocturnally foraging skinks and recorded cases of nocturnal activity in skinks have been reported in species and populations from the North Island, most on low-lying offshore northern islands (Towns 1999). There appears to be no geographic variation in activity patterns for the geckos, as seen in the skinks (KM Hare unpublished data). Whether altitude influences activity patterns among New Zealand's lizard species has not been investigated, nor have patterns over over winter.

With these daily activity patterns in mind, it is not surprising that, when compared with review data for activity of lizards worldwide (Vitt et al. 2003), New Zealand's endemic lizards do not adhere to general trends. For example, globally ~62 % of geckos are classed as nocturnal, ~36 % as diurnal and ~2 % as 'both'. Currently, New Zealand geckos have only 28 % recorded as nocturnal foragers, 21 % as diurnal foragers and 49 % as primarily nocturnal foragers that have been recorded out by day (e.g. basking, Hare and Cree 2016; Fig. 6.1e). Similarly, globally ~2 % of Autarchoglossa are classified as nocturnal, ~97 % as diurnal and 1 % as both nocturnal and diurnal, whereas 7 % of New Zealand's skinks are currently classified as nocturnally foraging, 8 % are nocturnally foraging with some diurnal behaviour, 77 % are diurnally foraging and 3 % are crepuscular, but also seen by day (Fig. 6.1f).

One way to determine the activity phase of lizards is by recording a time series. For example, a time series for *H. duvaucelli* from the Poor Knights Islands was developed from over 150 h of field observation from November to January across two seasons (Whitaker 1968). Whitaker (1968) observed that the geckos emerged at dusk, activity increased rapidly up till 2100 h, continuing until ~0330 h, after which the geckos began to seek retreats, with all in retreats by 0430 h. By day, the geckos retreated under stones, logs, bark and into rock crevices, hollow trees and petrel burrows. However, geckos were observed to bask in the sunlight where it fell near a retreat. Although mostly terrestrial in behaviour, they were sometimes predominantly arboreal where another species, such as *O. oliveri*, was present in high numbers. From these data, *H. duvaucelli* can be classified as a nocturnal forager with some diurnal emergence, with changes in habitat use with the presence of predators (see Sect. 6.5). As more data are collected on the lizards of New Zealand, their activity periods may be found to differ from those currently assigned, either as a species or as populations (e.g. with environmental temperature, latitude, altitude and/or the presence of certain predators and/or food sources).

6.4.2 Sociality, Courtship, Mating and Possible Parental Care

In lizards, sociality is generally agreed to be uncommon (Gardner et al. 2016), and parental care is even less commonly reported (Somma 2003). Some New Zealand lizards show social tendencies, although genetic studies are needed to confirm relatedness of individuals. For example, *O. otagense* are often seen in male–female pairs (Coddington and Cree 1997) and potentially family groups (Fig. 6.4c). Additionally, adult *W. maculata* have been observed assisting juveniles, suggesting possible social assistance and/or parental care (Hoare and Nelson 2006). Similarly, ~42 % of observed captive-held *O. maccanni* that have just given birth will bite open placental membranes that may enclose offspring at birth (Chamberlain et al. 2010), suggesting a rudimentary form of parental care.

Aggregative behaviour (where two or more conspecifics have concurrently overlapping home ranges) is another form of sociality and in squamates is generally formed to avoid predators, where insufficient retreats are present and/or as a way to control heat or water flux (Brattstrom 1974; Shah et al. 2003). To date, only 94 of ~9905 squamate species have been recorded as forming an aggregation (Gardner et al. 2016; Uetz and Hosek 2016). Aggregations of communally basking *O. acrinasum* have been observed in coastal Fiordland, with up to 12 skinks of all sizes intertwined in piles, suggesting potential thermal benefits (Thomas 1985). In contrast, some nocturnally foraging diplodactylid geckos form diurnal aggregations that consist of male–female pairs (sometimes with juveniles), or a mix of adults and juveniles (Fig. 6.3d; e.g. Hare and Hoare 2005; Barry et al. 2014). These gecko aggregations have been reported to include up to 200 individuals (Bauer 1990) and are formed in environments that appear to have many retreat sites available. Occurrence of aggregations despite the presence of multiple (apparently) suitable retreat sites implies a complex social system and/or other benefits (Shah et al. 2003; Hare and Hoare 2005; Barry et al. 2014). Of interest, no *H. duvaucelii* aggregations contain multiple males, and males with multiple females are larger than males forming single male:female pairs. This suggests that in *H. duvaucelii*, if sex-specific grouping patterns are related to mating, then larger males might be guarding females, and excluding smaller males, thereby potentially gaining mating advantages (Barry et al. 2014). However, the high variance in adult sex ratios within aggregations among different diplodactylid species (e.g. Hare and Hoare 2005) suggests that aggregations may not always represent family groups and/or harems. Additionally, no *Naultinus* geckos have been observed forming aggregations in the wild. Aggregation may be widespread and frequent in the diplodactylid geckos of New Zealand, but its taxonomic distribution, and purpose, needs clarification.

Courtship is generally a stereotypical sequence of behaviours that leads to mating. Although courtship behaviour is well studied in many vertebrates (e.g. birds), including many lizards overseas (Jenssen 1977), little is known about the courtship behaviour of New Zealand lizards. The most in-depth description for courtship behaviour for the gecko *W.* cf. *brunnea*, for which a list of eight stereotypical behaviours were identified: (1) Male approaches female jerkily or hesitantly; (2) Female approaches male jerkily or hesitantly; (3) Male trembles/shakes his head or body at the female; (4) Female trembles/shakes her head or body at the male; (5) Male sits on female's back and holds or nibbles her; (6) Male sits on female's back and bites her firmly in the flank or back of the neck; (7) One individual licks the other's cloaca. (8) Male on female's back with tails entwined/mating (Todd 2005).

In this species, larger males generally courted females more often, and males were observed courting up to four different females on the same day, suggesting that the mating system for this species is polygynandrous (Todd 2005).

For skinks, copulatory behaviour has been recorded only in wild *O. smithi*, where Whitaker (1968) wrote the following:

> two lizards were [observed] circling each other when first noticed. The male then approached the female, seized the side of her neck in his jaws, and thrust the lower part of his body under her tail so that their vents were pressed together [. . .]. After a few seconds the female wriggled free and scuttled off into the scrub, followed moments later by the male. (Whitaker 1968)

Perhaps New Zealand skinks follow a stereotypical sequence of courtship behaviours, but an ethogram has yet to be developed for any species of *Oligosoma*. Copulation position for skinks has been illustrated in captive *Oligosoma* (as [*Leiolopisma zelandica*]), with the male appearing to insert a hemipene from one side of the tail (Barwick 1959). This position has also been observed in *O. grande* (see Fig. 6.3a). Male squamates from elsewhere in the world often show a preference for using the right or left hemipene, and this may be true for New Zealand skinks and geckos, but requires further observations to confirm (Shine et al. 2000).

The mating system of most *Oligosoma* skinks is unknown. The most in-depth studies are for populations of *O. grande* at Macraes Flat, Otago. Observations of mating suggested a polygynous mating system, with males visiting several females sequentially (Eifler and Eifler 1999a). However, genetic studies showed that *O. grande* is in fact promiscuous, with approximately half of females and three quarters of males having more than one partner in a breeding season (Berry 2005). Additionally, around 18 % of offspring resulted from mating of related individuals, and related adults were often present on the same rock tor; proportions of related

Fig. 6.4 Some behaviours of endemic lizards of New Zealand. (**a**) Copulation of *Oligosoma grande*; the male is biting the side of the female, with his tail curled under and inseminating her presumably via his left hemipene (Photo: © James Reardon). (**b**) The nocturnally foraging gecko *Woodworthia* 'Otago large' basking by day at the entrance to a rock crevice (Photo: © Riki Mules). (**c**) Aggregation of five basking *Oligosoma otagense*, including two adults and three juveniles (Photo: © James Reardon). (**d**) Large aggregation of *Woodworthia maculata* within a bird nesting box; included are males, females and juveniles (Photo: © Dylan van Winkel)

individuals inhabiting the same rock tor did not differ between modified (agricultural) and native tussock grasslands (Berry 2005). Despite some antagonistic interactions among the adults, young lizards (<1 year) commonly shared crevices and maintained physical contact with adults without eliciting any obvious antagonistic response from adults (Eifler and Eifler 1999a).

6.4.3 Aggression and Competition

Typically, aggressive encounters within species are stereotypical to reduce the possibility of damage and death. Among skinks, aggressive encounters often begin by way of a slow vibration of the tail tip (e.g. Torr and Shine 1994). A typical combat sequence has been recorded in captive *O. suteri* (Towns 1975) and involves: (1) opponents sight each other, and Male-A (lower ranked) begins to vibrate his tail; (2) Male-B (higher ranked) bites vibrating tail at tail base; (3) Male-A bites neck of Male-B causing him to release tail base; (4) Male-A then flees with his tail still vibrating and Male-B in pursuit (Towns 1975). *Oligosoma* skinks have been observed undergoing aggressive encounters during the breeding season and over finite resources (e.g. Eifler and Eifler 1999a), although there appears to be a spectrum of aggression among skinks. At one end are the apparently social skinks (see Sect. 6.4.1), moving through the more territorial species, such as *O. inconspicuum* (often scarred from aggressive encounters which include mainly chasing and biting behaviours, although other behaviours included head butting and tail lashing; Patterson 1992), through to those species that are difficult to keep in captivity due to individuals killing each other during aggressive encounters (e.g. *O. macgregori*; Newman 1994).

Competition is where the interaction between organisms or species results in reduced biological fitness of one when the other is present; limited supply of a resource (e.g. food, water and territory) is seen as a key factor (Downes and Bauwens 2001). Thus, competition among and within species is often inferred by niche separation (discussed earlier in Sect. 6.2). For example, although some *H. duvaucelii* populations tolerate retreat sharing with other species (Whitaker 1968), competition among species for access to sugar sources on Korapuki Island, Mercury Island group, influences their habitat use (Evans et al. 2015). In particular, *W. maculata* avoid trees with high populations of the larger gecko *H. duvaucellii* (Evans et al. 2015), and juvenile *W. maculata* avoid sugar sources used by larger adults, indicating competition between different age classes within a species (Evans et al. 2015). Whether these patterns are related to competition per se (biological fitness) and/or potential predator avoidance (see Sect. 6.5 for more discussion) is unclear and warrants further investigation. Competition with introduced pests has also been reported (e.g. European wasps (*Vespula germanica*) drink honeydew Nelson et al. 2016 for review of this topic).

6.5 Defence and Predators

6.5.1 Defence Tactics of New Zealand's Lizards

Most animals undergo fight or flight responses in response to danger. In response to humans (a predator of native lizards; Natusch 1979), *Naultinus* geckos may freeze, using crypsis as camouflage, and, if approached, may drop to the ground to flee (Hitchmough 1979). If cornered, some *Naultinus* may elevate their posture, arching their backs and standing on toes, opening their mouths in a wide gape to show the brightly coloured inside (Box 6.2; Woodward 1941). When handled, both skinks and geckos will generally writhe and frequently bite (e.g. *O. oliveri* and *H. duvaucelii*, Whitaker 1968). Some species of skinks and geckos make vocalisations during handling (e.g. *O. homalonoton*, Towns and McFadden 1993), and some geckos and skinks have been heard vocalising within their retreats (Box 6.2). Flight responses generally include dashing to the nearest retreat, and for some skinks and geckos that live near the water, this may be into the water itself

Box 6.2 Vocalisations & threat display

Several species of New Zealand's lizards vocalise. For example, the skink *Oligosoma homalonotum* 'squeaks' when disturbed or handled (the latter often accompanied by mouth gapes and biting; Towns & McFadden 1993), and *O. acrinasum* 'squeak' while evading capture and during refuge sharing (Thomas 1985). However, the geckos have more vocal ability, which is unsurprising considering that vocalisations are well documented in geckos overseas (e.g. Werner 1973). The vocal repertoire of New Zealand's geckos range from faint chirps and squeaks to loud croaks and barks (McCann 1955; Whitaker 1982). These vocalisations are classified as 'distress' or 'social' calls.

Defence posture of *Naultinus punctatus* showing the bright blue inside of the mouth (Photo: © James Reardon)

Distress calls probably evolved to delay a predatory attempt and/or to surprise a predator into relaxing its grasp, both enabling escape. Distress calls can be very loud, some heard up to 10 m away (e.g., Hitchmough 1979), and are recorded in many species of *Naultinus*. Two types of distress call have been recorded: (i) a short-duration single burst of frequency ~4,500 – 5,000 hz; (ii) a fast series of regularly spaced short chirps (Hitchmough 1979). The former is often associated with defensive posturing, whereby the inflated body is raised high, the throat distended and the mouth opened wide to reveal the often brightly coloured interior (see picture above right). Defensive elevated posturing is often accompanied by vigorous tail movements, aggressive lunges and loud vocalisations (Woodward 1941). At lower environmental temperatures often less stimulus is needed to evoke the defensive call and posture (Whitaker 1970).

A range of other vocalisations have been reported in geckos, some of which appear to be social in nature. For example, after a male *Woodworthia* 'Otago Large' was introduced to a cage of several females, chattering was heard a few minutes later (Alison Cree pers. comm). Finally, analysis of the voice indicates that the genera *Naultinus* and *Mokopirirakau* can be 'easily separated' (Whitaker 1982), suggesting species-specific repertoires.

To hear vocalisation of *Naultinus rudis* visit:
https://www.youtube.com/watch?v=kF720e7zW0k

Box 6.2 Vocalisations and threat display

(see Hare and Miller 2009 for review). Species may also change their behaviour and habitat use in the presence of predators and/or competitors. For example, *H. duvaucelli* use different microhabitats in the presence of *Rattus exulans* (Hoare et al. 2007).

When evasion and escape fail to deter threats, lizards use their major (final) defence mechanism, which is caudal autotomy; involving breaking and discarding the tail at predetermined fracture planes. However, autotomy can occur during aggressive intraspecific encounters, and some lizard species shed their tail without direct contact with a predator (Arnold 1984). Thus, care should be taken when using prevalence of previous tail loss as an indicator of predatory interactions. Autotomy may enable the lizard to flee and also provides a spontaneously moving distraction (Arnold 1988). The benefit of caudal autotomy is thus immediate survival, and over time lizards can regenerate their tails. However, autotomy also induces physiological and functional costs, including reduced: reproductive output, growth rate, locomotor performance, social status, mating opportunities and probability of future survival (see Hare and Miller 2010 and references within). Thus, lizards will exhibit crypsis, escape and an aggressive response prior to resorting to tail autotomy (Arnold 1988). Reported tail loss in the field can be high. For example, 95 % of *O. fallai*, 90 % of *O. ornatum* and 92 % of *D.* 'Three Kings', on the Three Kings Islands had regenerating tails (Parrish and Gill 2003). Tail autotomy appears to be lower in arboreal species such as *Naultinus* geckos (e.g. tail loss of *N. manukanus* from Stephens Island ranged from 10 to 14 % of the sampled population; Hare et al. 2007). However, whether these patterns of tail loss with microhabitat use are ubiquitous requires further investigation. In some New Zealand lizards, predation pressure and/or social interactions, rather than innate disposition, probably influences the field rates of tail loss (Hare and Miller 2010).

6.5.2 Predators of New Zealand's Lizards

Lizards are a key component in the diet of many predatory species, and 50 species have been reported as predators of New Zealand's lizards, including five invertebrates (Table 6.2). Internationally, birds are considered the most frequent predator of reptiles (Martín and López 1996). In New Zealand, birds comprise 51 % of species reported to prey on lizards (18 native and seven introduced bird species; Table 6.2). However, the intensity of predation among species varies, with some birds specialising in hunting lizards at certain times of the year. For example, the sacred kingfisher (*Todiramphus sanctus*) is an avid predator of lizards, especially during the breeding season (see Nelson et al. 2016 for details). Lizards are also a key component of New Zealand's fauna (see Towns et al. 2016), and six species of New Zealand's lizards have been recorded to prey upon other lizard species in the wild, often only consuming the autotomized tail (see Sect. 6.3; Fig. 6.3d; Table 6.1, 6.2). However, in New Zealand, predation by introduced mammals is of greater conservation concern (see Towns et al. 2016 and Nelson et al. 2016 for more discussion). Evidence of detrimental impacts by mammals includes: (1) greater species diversity and population density of lizards on mammal-free islands than unmanaged mainland sites; (2) where mammals are exterminated from islands, or reduced to very low numbers on the mainland, positive responses such as increase in the range of habitats occupied, population densities and reproductive success of lizards is observed (Towns and Daugherty 1994; Towns 1996; Reardon et al. 2012).

Almost all introduced mammalian predators are reported as preying upon lizards (Table 6.2), with high rates of lizard consumption reported in some mammals. For example, the stomach contents of a cat (*Felis catus*) from Macraes Flat, Otago, held 14 lizards from one morning's hunting effort, including threatened species (Daugherty and Towns 1991). This report is not a one-off event, or even the maximum number recorded. Predation by cats was first described in 1870, where 36 lizards were found in the stomach of a feral cat (Taylor 1870). Mice (*Mus musculus*) have been observed directly attacking lizards (Newman 1994) and with lizards in stomach contents (Wedding 2007). However, stomach contents and faeces used for analyses of dietary components only reveal recent intake, whereas stable isotopes and/or DNA analyses can provide a less biased cumulative account of consumption (e.g. Janssen et al. 2015). Although the common brushtail possum (*Trichosurus vulpecula*) is reported to prey upon vertebrates such as birds (e.g. Brown et al. 1993), we found no published evidence of their predation on lizards. Non-predatory mammals may also impact lizard abundance and survival. For example, intense grazing by European rabbits (*Oryctolagus cuniculus*) reduces shelter and food availability for lizards (Norbury 2001), and control of rabbits without control of predatory mammals also results in predators switching to prey more heavily on skinks (Norbury 2001).

Introduced amphibians and invertebrates also prey upon New Zealand's lizards (Table 6.2), including European wasps (Nelson et al. 2016; Table 6.2). In unnatural situations (e.g. captivity and field traps), species that may not normally be capable of capturing lizards can become predators. For example, endemic crabs (*Leptograpsus variegatus*) have been observed killing and consuming lizards trapped within pitfall traps (D. Towns unpub. data). Of interest is a report of a lizard in the stomach of a caught marine fish (Anonymous 2003), which suggests the lizard may have been in the water either hunting for prey (e.g. Whitaker 1968), seeking refuge from predators (e.g. Hare and Miller 2009), accidently after being washed off rocks or actively dispersing. Finally, sex-biased predation pressure may exist. For example, more pregnant female *O. maccanni*, than males, were recorded in the diet of cats (Middlemiss 1995). Pregnant or gravid female lizards may be most at risk from behaviours such as avid sun basking, and also their changed shape and reduced locomotor capacity (Hare and Cree 2016), but this needs further investigation.

Table 6.2 Organisms recorded as preying upon endemic lizards of New Zealand in the wild

Description	Order	Species	Skinks	Geckos	Source (examples only)
Native birds	Accipitriformes	Swamp harrier (*Circus approximans*)	●	●	Pierce and Maloney (1989) and Whitaker (1972)
	Charadriiformes	Black-fronted tern (*Chlidonias albostriatus*)	●		O'Donnell and Hoare (2009)
	Charadriiformes	Red-billed gull (*Larus novaehollandiae*)	☐	☐	Oliver (1955)
	Coraciiformes	Sacred kingfisher (*Todiramphus sanctus*)	●	●	Fitzgerald et al. (1986)
	Cuculiformes	Long-tailed cuckoo (*Eudynamys taitensis*)	●		Falla et al. (1966)
	Gruiformes	Banded rail (*Gallirallus philippensis*)	●		Stephenson et al. (1966)
	Gruiformes	Pukeko (*Porphyrio melanotus*)	◊	◊	Muggeridge and Cottier (1931) and Carroll (1966)
	Gruiformes	Takahe (*Porphyrio hochstetteri*)	●	●	Whitaker (1991)
	Gruiformes	Weka (*Gallirallus australis*)	◊	●	Potts (1871), Coleman et al. (1983) and Thomas (1982)
	Laridae	Southern black-backed gull (*Larus dominicanus*)	☐	☐	Oliver (1955)
	Falconiformes	New Zealand falcon (*Falco novaeseelandiae*)	●	●	Fox (1977)
	Passeriformes	New Zealand pipit (*Anthus novaeseelandiae*)	◊	◊	Wilkinson and Wilkinson (1952)
	Passeriformes	North Island fernbird (*Bowdleria punctata*)	●		Ball and Parrish (2005)

(continued)

Table 6.2 (continued)

Description	Order	Species	Skinks	Geckos	Source (examples only)
	Pelecaniformes	Australasian bittern (*Botaurus poiciloptilus*)	◻	◻	Buddle (1951)
	Pelecaniformes	White-faced heron (*Egretta novaehollandiae*)	●		Pierce (1980)
	Psittaciformes	Kakapo (*Strigops habroptilus*)	◇	◇	von Hugel (1875)
	Strigiformes	*Laughing owl (*Sceloglaux albifacies*)	◇	◇	S[mith] (1884)
	Strigiformes	Morepork (*Ninox novaeseelandiae*)	●	●	Chambers et al. (1955) and Parrish and Gill (2003)
Introduced birds	Galliformes	Domestic fowl (*Gallus gallus)*	●		Bell (1996)
	Halcyonidae	Laughing kookaburra (*Dacelo novaeguineae*)	◇	◇	O'Brien (1981)
	Passeriformes	Blackbird (*Turdus merula*)	●		Bell (1996)
	Passeriformes	Common starling (*Sturnus vulgaris*)	●		Thompson (2000)
	Passeriformes	Common myna (*Acridotheres tristis*)		●	Whitaker (1972)
	Passeriformes	Australasian magpie (*Gymnorhina tibicen*)	●	●	Whitaker (1972) and McIlroy (1968)
	Strigiformes	Little owl (*Athene noctua*)		●	Marples (1942)
Native herpetofauna	Rhynchocephalia	Tuatara (*Sphenodon punctatus*)	●	●	Walls (1982)
	Squamata	Cryptic skink (*Oligosoma inconspicuum*)	○		Patterson (1992)
	Squamata	Duvaucel's gecko (*Hoplodactylus duvaucelii)*		●	Barwick (1982)
	Squamata	McCann's skink (*Oligosoma maccanni*)	○		Patterson (1992)

(continued)

Table 6.2 (continued)

Description	Order	Species	Skinks	Geckos	Source (examples only)
	Squamata	Otago skink (*Oligosoma otagense*)	●		Tocher (2003)
	Squamata	Spotted skink (*Oligosoma lineoocellatum* 'Central Canterbury')	●		Allison and Desser (1981)
	Squamata	Robust skink (*Oligosoma alani)*		●	Southey (1985b)
Introduced herpetofauna	Anura	Southern bell frog (*Litoria raniformis*)	○		Romijn (2007)
Introduced mammals	Artiodactyla	Pigs (*Sus scrofa)*	□	□	King (1995)
	Carnivora	Domestic cat (*Felis catus*)	●	●	Gibb et al. (1969) and Karl and Best (1982)
	Carnivora	Domestic dog (*Canis lupis*)	●		Whitaker (1972)
	Carnivora	Ferret (*Mustela furo*)	●	●	Fitzgerald (1964) and Whitaker (1972)
	Carnivora	Stoat (*Mustela erminea*)	●	●	King and Moody (1982)
	Carnivora	Weasel (*Mustela nivalis vulgaris*)	●	●	King and Moody (1982)
	Eulipotyphla	European hedgehog (*Erinaceus europaeus*)	●	●	Jones et al. (2005)
	Rodentia	House mouse (*Mus musculus*)	●		Pickard (1984)
	Rodentia	Kiore (*Rattus exulans)*	●	○	Bettesworth (1972b) and Dick (1985)
	Rodentia	Norway rat (*Rattus norvegicus*)	●	○	Bettesworth (1972a) and Dick (1985)
	Rodentia	Black rat (*Rattus rattus)*	○	○	Towns et al. (2006)
Native invertebrates	Scolopendromorpha	Giant centipede (*Cormocephalus rubriceps*)	●	●	Southey (1985a)

(continued)

Table 6.2 (continued)

Description	Order	Species	Skinks	Geckos	Source (examples only)
	Coleoptera	Carabid beetle (*Megadronas hanmerensis*)	●		Whitaker (1972)
	Araneae	Katipo spider (*Latrodectus katipo*)	●		Lettink and Patrick (2006)
Introduced invertebrates	Hymenoptera	Common wasp (*Vespula vulgaris*)	□	□	Thomas (1987)
	Hymenoptera	European wasp (*Vespula germanica*)	□	□	Thomas (1987)

Filled circle = recorded actively preying upon lizard and/or in stomach contents, scats and/or by stable isotopes; *unfilled circle* = inferred as in diet by authors and/or where lizard numbers decrease in the presence of organism; *diamond* = where authors record 'lizards' in diet and therefore may be a gecko, skink or both; *square* = where stated as predators, but evidence has not been provided; *asterisk* = extinct

6.6 Conclusions

With around half (45 %) of the 104 endemic species of lizard in New Zealand yet to be formally described, assumptions of biology and ecology have often been made about species based on the ecology of similar, well-known species (e.g. activity period of geckos). What we do know for most species are broad generalisations, with some overlap among a few species, and a few in-depth studies. We can safely conclude that nearly every available habitat from coast to mountain top, and from north to south, has at least one lizard species present. High levels of sympatry exist in some locations, particularly offshore islands where these species partition resources at spatial, temporal and trophic scales. However, some species also show competition and/or aggression and may even prey upon each other. New Zealand lizards appear to have a highly opportunistic dietary strategy, eating whatever is available in the environment, although a few appear to specialise at certain times of the year (e.g. *O. grande* eating flower petals). The lizards of New Zealand also appear to form a key component of the diet of many native and introduced species. Many lizards will form aggregations, and these may be family groupings; parental care is also possible.

For all these trends and generalisations, we still need more information to enable trends in ecology, behaviour and evolution to be described. Additionally, increased understanding of such a large and diverse group of New Zealand's fauna may shed light on the evolution of New Zealand's largest vertebrate group (Towns et al. 2016) and provide much needed information for their effective conservation in situ. Although a daunting prospect, we challenge researchers to continue collecting, recording and (importantly) publishing various aspects of the ecology of all species. Some particular areas of research that would benefit from more data have been scattered throughout the text, as a starting point for future studies.

Acknowledgements We are grateful to Ben Bell, Anna Carter, Sarah Herbert, Zoë Lennon, Sue Keall, Riki Mules, Nicky Nelson, Stephanie Price, Patty Ramirez and Chris Woolley, for comments on the draft chapter. We also thank KC (Kevin) Burns, Alison Cree, Rod Hitchmough and Marieke Lettink for useful discussions and thank Alison Cree and Riki Mules for their personal communications. Finally, we are very grateful to the following for permission to use their photographs: Marieke Lettink, Riki Mules, Rod Morris, James Reardon and the New Zealand Department of Conservation Grand and Otago Skink Recovery Programme.

References

Allison B, Desser SS (1981) Developmental stages of *Hepatozoon lygosomarum* (Doré 1919) comb. n. (Protozoa: Haemogregarinidae), a parasite of a New Zealand skink, *Leiolopisma nigriplantare*. J Parasitol 67:852–858

Anonymous (2003) Lizards as snapper bait? New Zealand Fishing News. Rugby Press, Auckland

Arnold EN (1984) Evolutionary aspects of tail shedding in lizards and their relatives. J Nat Hist 18:127–169

Arnold EN (1988) Caudal autotomy as a defense. In: Gans C, Huey RB (eds) Biology of the Reptilia, vol 16, Defense and life history. Alan R. Liss, Inc, New York, p 659

Ball OP, Parrish R (2005) Lizard predation by North Island fernbird (*Bowdleria punctata vealeae*). Notornis 52:250–251

Barr BP (2009) Spatial ecology, habitat use, and the impacts of rats on chevron skinks (*Oligosoma homalonotum*) on Great Barrier Island. Unpublished MSc thesis, Massey University, Auckland

Barry M, Shanas U, Brunton DH (2014) Year-round mixed-age shelter aggregations in Duvaucel's geckos (*Hoplodactylus duvaucelii*). Herpetologica 70:395–406

Barwick RE (1959) The life history of the common New Zealand skink *Leiolopisma zelandica* (Gray, 1843). Trans R Soc N Z 86:331–380

Barwick RE (1982) The growth and ecology of the gecko *Hoplodactylus duvaucelii* at The Brothers Islands. In: Newman DG (ed) New Zealand herpetology, vol 2. New Zealand Wildlife Service, Occasional Publication, Wellington, pp 377–398

Bauer AM (1990) Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). Bonn Zool Monogr 30:1–218

Bell BD (1996) Blackbird (*Turdus merula*) predation on the endemic copper skink (*Cyclodina aenea*). Notornis 43:213–217

Berry OF (2005) Inbreeding and promiscuity in the endangered grand skink. Conserv Genet 7:427–437

Berry O, Tocher MD, Gleeson DM, Sarre SD (2005) Effect of vegetation matrix on animal dispersal: genetic evidence from a study of endangered skinks. Conserv Biol 19:855–864

Bettesworth DJ (1972a) Aspects of the ecology of *Rattus norvegicus* on Whale Island, Bay of Plenty, New Zealand. Unpublished MSc thesis, University of Auckland, Auckland

Bettesworth DJ (1972b) *Rattus exulans* on Red Mercury Island. Tane 18:117–118

Brattstrom BH (1974) The evolution of reptilian sociality. Am Zool 14:35–45

Brown K, Innes J, Shorten R (1993) Evidence that possums prey on and scavenge birds' eggs, birds and mammals. Notornis 40:169–177

Buddle PC (1951) Bird secrets. AH & AW Reed, Wellington

Carroll ALK (1966) Food habits of pukeko (*Porphyrio melanotus* Temmink). Notornis 13:133–142

Chamberlain AJ, Cree A, Hare KM (2010) Mysterious moments: unveiling birth in a viviparous lizard. N Z J Zool 37:65

Chambers BS, Chambers S, Sibson RB (1955) Notes on the Hen and Chicken Islands. Notornis 6:152–157

Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Bell TP, Chapple SNJ, Miller KA, Daugherty CH, Patterson GB (2011) Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma inconspicuum*; Reptilia: Scincidae) species complex. Zootaxa 2782:1–33

Christmas E (1995) Interactions between Duvaucel's gecko (*Hoplodactylus duvaucelii*) and kiore (*Rattus exulans*). Unpublished MSc thesis, University of Otago, Dunedin

Coddington E, Cree A (1997) Population numbers, response to weather, movements and management of the threatened New Zealand skinks *Oligosoma grande* and *O. otagense* in tussock grasslands. Pac Conserv Biol 3:379–391

Coleman JD, Warburton B, Green WQ (1983) Some population statistics and movements of the western weka. Notornis 30:93–107

Conway BH, Gaynor DJ (1979) The Lewis Pass Scenic Reserve. Unpublished report, New Zealand Department of Lands and Survey, Christchurch

Cree A (1994) Low annual reproductive output in female reptiles from New Zealand. N Z J Zool 21:351–372

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Daugherty CH, Towns DR (1991) The cat's breakfast. N Z Sci Mon April:13–14

Daugherty CH, Towns DR, Atkinson IAE, Gibbs GW (1990) The significance of the biological resources of New Zealand islands for ecological restoration. In: Towns DR, Daugherty CH, Atkinson IAE (eds) Ecological restoration of New Zealand Islands, Conservation Science Publication no. 2. Department of Conservation, Wellington, pp 9–21

Dick AMP (1985) Rats on Kapiti Island, NZ: coexistence and diet of *Rattus norvegicus* Berkenhout and *Rattus exulans* Peale. Massey University, Palmerston North

Downes S, Bauwens D (2001) An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species. Anim Behav 63:1037–1046

Duncan P (1999) Behavioural and ecological factors affecting the trappability of two skinks species in Nelson. Unpublished MSc thesis, University of Otago, Dunedin

Efford MG, Spencer NJ, Thomas BW, Mason RFS (1997) A population study of sympatric skinks on Lake Station, upper Buller Valley. N Z J Zool 24:326

Eifler DA (1995) Patterns of plant visitation by nectar-feeding lizards. Oecologia 101:228–233

Eifler DA, Eifler MA (1999a) Foraging behavior and spacing patterns of the lizard *Oligosoma grande*. J Herpetol 33:632–639

Eifler DA, Eifler MA (1999b) The influence of prey distribution on the foraging strategy of the lizard *Oligosoma grande* (Reptilia: Scincidae). Behav Ecol Sociobiol 45:397–402

Evans AE, Towns DR, Beggs RJ (2015) Relative importance of sugar resources to endemic gecko populations in an isolated island ecosystem. N Z J Ecol 39:262–272

Falla RA, Sibson RB, Turbott EG (1966) A field guide to the birds of New Zealand. Collins, London

Fitzgerald BM (1964) Ecology of mustelids in New Zealand. Unpublished MSc thesis, University of Canterbury, Christchurch

Fitzgerald BM, Meads MJ, Whitaker AH (1986) Food of the kingfisher (*Halcyon sancta*) during nesting. Notornis 33:23–32

Flannagan HJ (2000) Conservation biology of the Goldstripe gecko (*Hoplodactylus chrysosireticus*) and interactions with Duvaucel's gecko (*Hoplodactylus duvaucelii*) on Mana Island, Cook Strait, New Zealand. Unpublished MSc thesis, Massey University, Palmerston North

Fleming CA (1939) Birds of the Chatham Islands. Emu 38:380–413

Fox NC (1977) The biology of the New Zealand falcon (*Falco novaeseelandiae* Gmelin 1788). University of Canterbury, Christchurch

Freeman AB (1994) An ecological study of the lizard fauna of Kaitorete Spit, Canterbury. Unpublished MSc thesis, Lincoln University, Christchurch

Freeman AB (1997) Comparative ecology of two *Oligosoma* skinks in coastal Canterbury: a contrast with central Otago. N Z J Ecol 21:153–160

Gardner MG, Pearson SK, Johnston GR, Schwarz MP (2016) Group living in squamate reptiles: a review of evidence for stable aggregations. Biol Rev. doi: 10.1111/brv.12201. [online early]

Gebauer K (2012) Dynamics of grand skink (*Oligosoma grande*, Gray 1945) metapopulations in indigenous tussock grasslands and exotic pasture grasslands in southern New Zealand. Unpublished PhD thesis, University of Otago, Dunedin

Germano JM (2005) Home ranges, movements, and effects of capture on the Otago skink (*Oligosoma otagense*). N Z J Zool 32:222

Germano JM, Bishop PJ (2008) Suitability of amphibians and reptiles for translocation. Conserv Biol 23:7–15

Gibb JA, Ward GD, Ward CP (1969) An experiment in the control of a sparse population of wild rabbits (*Oryctolagus c. cuniculus* L.) in New Zealand. N Z J Sci 12:509–534

Gibbs G (2006) Ghosts of Gondwana: the history of life in New Zealand. Craig Potton Publishing, Nelson

Gibson S, Penniket S, Cree A (2015) Are viviparous lizards from cool climates ever exclusively nocturnal? Evidence for extensive basking in a New Zealand gecko. Biol J Linn Soc 115:882–895

Gill BJ (1976) Aspects of the ecology, morphology, and taxonomy of two skinks (Reptilia: Lacertilia) in the coastal Manawatu area of New Zealand. N Z J Zool 3:141–157

Hare KM, Cree A (2005) Natural history of *Hoplodactylus stephensi* (Reptilia: Gekkonidae) on Stephens Island, Cook Strait, New Zealand. N Z J Ecol 29:137–142

Hare KM, Cree A (2016) Thermal and metabolic physiology of New Zealand lizards. Chap. 9. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hare KM, Hoare JM (2005) *Hoplodactylus maculatus* (common gecko) aggregations. Herpetol Rev 36:179

Hare KM, Miller KA (2009) What dives beneath: diving as a measure of performance in lizards. Herpetologica 65:227–236

Hare KM, Miller KA (2010) Frequency of tail loss does not reflect innate predisposition in temperate New Zealand lizards. Naturwissenschaften 97:197–203

Hare KM, Hoare JM, Hitchmough R (2007) Investigating natural population dynamics of *Naultinus manukanus* to inform conservation management of New Zealand's cryptic diurnal geckos. J Herpetol 41:80–92

Harper PC (1983) Biology of the Buller's shearwater (*Puffinus bulleri*) at the Poor Knights Islands, New Zealand. Notornis 30:299–318

Hitchmough RA (1979) The ecology and behaviour of two green gecko (*Naultinus*) species. Unpublished MSc thesis, University of Auckland, Auckland

Hitchmough RA (1982) The ecology of a population of *Naultinus grayii* Bell near Kaitaia. In: Newman DG (ed) New Zealand herpetology. New Zealand Wildlife Service Department of Internal Affairs, Occasional Publication No. 2, Wellington, pp 399–407

Hitchmough R, Barr B, Lettink M, Monks J, Reardon J, Tocher M, van Winkel D, Rolfe J (2016a) Conservation status of New Zealand reptiles, 2015. New Zealand Department of Conservation, Wellington

Hitchmough RA, Patterson GB, Chapple DG (2016b) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hoare JM, Nelson NJ (2006) *Hoplodactylus maculatus* (common gecko) social assistance. Herpetol Rev 37:222–223

Hoare JM, Stephens CL, Daugherty CH, Phillpot PMS (2005) *Oligosoma lineoocellatum* (spotted skink). Longevity, site fidelity. Herpetol Rev 36:181

Hoare JM, Pledger S, Nelson NJ, Daugherty CH (2007) Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. Biol Conserv 136:510–519

Hoare JM, Melgren P, Chavel EE (2013) Habitat use by southern forest geckos (*Mokopirirakau* 'Southern Forest') in the Catlins, Southland. N Z J Zool 40:129–136

Janssen J, Towns DR, Duxbury M, Heitkonig I (2015) Surviving in a semi-marine habitat: dietary salt exposure and salt excretion of a New Zealand intertidal skink. Comp Biochem Physiol A 189:21–29

Jenssen TA (1977) Evolution of anoline lizard display behaviour. Am Zool 17:203–215

Jones C, Moss K, Sanders K (2005) Diet of hedgehogs (*Erinaceus europaeus*) in the upper Waitaki Basin, New Zealand: implications for conservation. N Z J Ecol 29:29–35

Karl BJ, Best HA (1982) Feral cats on Stewart Island; their foods, and their effects on kakapo. N Z J Zool 9:287–294

King CM (ed) (1995) The handbook of New Zealand mammals. Oxford University Press, Auckland

King CM, Moody JE (1982) The biology of the stoat (*Mustela erminea*) in the National parks of NZ II. Food habits N Z J Zool 9:57–80

Knox CD, Monks JM (2014) Penning prior to release decreases post-translocation dispersal of jewelled geckos. Anim Conserv 17:18–26

Le Gouar P, Mihoub J-B, Sarrazin F (2012) Dispersal and habitat selection: behavioural and spatial constraints for animal translocations. In: Ewen JGA, Armstrong DP, Parker KA, Seddon PJ (eds) Reintroduction biology: integrating science and management. Wiley-Blackwell, Oxford, pp 138–164

Lettink M (2007) Detectability, movements and apparent lack of homing in *Hoplodactylus maculatus* (Reptilia: Diplodactylidae) following translocation. N Z J Ecol 31:111–116

Lettink M, Hare KM (2016) Sampling techniques for New Zealand lizards. Chap. 10. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Lettink M, Patrick BH (2006) Use of artificial cover objects for detecting red katipo, *Latrodectus katipo* Powell (Araneae: Theridiidae). N Z J Entomol 29:99–102

Liggins L, Chapple DG, Daugherty CH, Ritchie PA (2008) A SINE of restricted gene flow across the Alpine Fault: phylogeography of the New Zealand common skink (*Oligosoma nigriplantare polychroma*). Mol Ecol 17:3668–3683

Marples BJ (1942) A study of the little owl, *Athene noctua*, in New Zealand. Trans Proc R Soc N Z 72:237–252

Marshall JM (1983) Homing and celestial orientation in two lizards *Hoplodactylus maculatus* and *Leiolopisma nigriplantare*. Unpublished BSc honours dissertation, Victoria University of Wellington, Wellington

Martín J, López P (1996) Avian predation on a large lizard (*Lacerta lepida*) found at low population densities in Mediterranean habitats: an analysis of bird diets. Copeia 1996:722–726

McCann C (1955) The lizards of New Zealand. Gekkonidae and Scincidae. Dominion Mus Bull 17:1–127

McIlroy JC (1968) The biology of magpies (*Gymnorhina* spp.) in New Zealand. Unpublished MSc thesis, Lincoln College, Christchurch

McIntyre NE, Wiens JA (1999) Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns. Landsc Ecol 14:437–447

Melgren P (1980) *Leiolopisma striatum* (Buller) is a rare and endangered species. Herpetofauna 11:12–14

Middlemiss A (1995) Predation of lizards by feral house cats (*Felis catus*) and ferrets (*Mustela furo*) in the tussock grassland of Otago. Unpublished MSc thesis, University of Otago, Dunedin

Miller KA, Bell TP, Germano JM (2014) Understanding publication bias in reintroduction biology by assessing translocations of New Zealand's herpetofauna. Conserv Biol 28:1045–1056

Molles M (2013) Ecology: concepts and applications, 6th edn. McGraw-Hill, Boston, MA

Montoya I, Burns KC (2007) Community-wide character displacement in New Zealand skinks. J Biogeogr 34:2139–2147

Muggeridge J, Cottier W (1931) Food habits of the pukeko. N Z J Sci Technol XIII:36

Natusch S (1979) Wild fare for wilderness foragers. Collins, Auckland

Neall VE, Trewick SA (2008) The age and origin of the Pacific Islands: a geological overview. Philos Trans R Soc B 363:3293–3308

Neilson K, Curran JM, Towns DR, Jamieson H (2006) Habitat use by chevron skinks (*Oligosoma homalonotum*) (Sauria: Scincidae) on Great Barrier Island, New Zealand. N Z J Ecol 30:345–356

Nelson NJ, Romijn RL, Dumont T, Reardon JT, Monks JM, Hitchmough RA, Empson R, Briskie JV (2016) Lizard conservation in mainland sanctuaries. Chap. 12. In: Chapple DG (ed) - New Zealand lizards. Springer, Cham

Newman DG (1994) Effects of a mouse, *Mus musculus*, eradication and habitat change on lizard populations of Mana Island, New Zealand, with special reference to McGregor's skink, *Cyclodina macgregori*. N Z J Zool 21:443–456

Newstrom L, Robertson A (2005) Progress in understanding pollination systems in New Zealand. N Z J Bot 43:1–59

Norbury G (2001) Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. J Appl Ecol 38:1350–1361

Nyhagen DF, Kragelund C, Olesen JM, Jones CG (2001) Insular interactions between lizards and flowers: flower visitation by an endemic Mauritian gecko. J Trop Ecol 17:755–761

O'Brien C (1981) A book of NZ wildlife—a guide to the native and introduced animals of New Zealand. Landsdowne Press, Auckland

O'Donnell CFJ, Hoare JM (2009) Predation of lizards by black-fronted terns (*Sterna albostriata*). Notornis 56:167–168

Olesen JM, Valido A (2003) Lizards as pollinators and seed dispersers: an island phenomenon. Trends Ecol Evol 18:177–181

Olesen JM, Valido A (2004) Lizards and birds as generalized pollinators and seed dispersers of island plants. In: Fernandez-Palacios JM, Morici C (eds) Ecologia Insular/Island ecology. Asociacion Espanola De Ecologia Terrestre (AEET) and Excmo, Cabildo Insular de La Palma, La Palma, pp 229–249

Oliver WRB (1955) New Zealand birds. AH & AW Reed, Wellington

Parrish GR, Gill BJ (2003) Natural history of the lizards of the Three Kings Islands, New Zealand. N Z J Zool 30:205–220

Patterson GB (1985) The ecology and taxonomy of the common skink *Leiolopisma nigriplantare maccanni* in tussock grasslands in Otago. Unpublished PhD thesis, University of Otago, Dunedin

Patterson GB (1992) The ecology of a New Zealand grassland lizard guild. J R Soc N Z 22:91–106

Patterson GB (1997) South Island skinks of the genus *Oligosoma*: description of *O. longipes* n. sp. with redescription of *O. otagense* (McCann) and *O. waimatense* (McCann). J R Soc N Z 27:439–450

Phillpot PMS (2000) The skinks of North Brother Island: abundance, habitat use and species interactions. Unpublished MSc thesis. Victoria University of Wellington, Wellington

Pianka ER, Vitt LJ (2003) Lizards: windows to the evolution of diversity. University of California Press, Los Angeles, CA

Pickard CR (1984) The population ecology of the house mouse (*Mus musculus*) on Mana Island. Unpublished MSc thesis, Victoria University of Wellington, Wellington

Pierce RJ (1980) Seasonal and long term changes in bird numbers at Lake Wainono. Notornis 27:21–44

Pierce RJ, Maloney RF (1989) Responses of harriers in the MacKenzie Basin to the abundance of rabbits. Notornis 36:112

Plummer MV, Mills NE (2000) Spatial ecology and survivorship of resident and translocated hognose snakes (*Heterodon platirhinos*). J Herpetol 34:565–575

Porter R (1987) An ecological comparison of two *Cyclodina* skinks (Reptilia: Lacertilia) in Auckland, New Zealand. N Z J Zool 14:493–507

Potts TH (1871) On the birds of New Zealand. Trans N Z Inst 3:59–109

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. Q Rev Biol 52:137–154

Reardon JT, Whitmore N, Holmes KM, Judd LM, Hutcheon AD, Norbury G, Mackenzie DI (2012) Predator control allows critically endangered lizards to recover on mainland New Zealand. N Z J Ecol 36:141–150

Robb J (1980) New Zealand amphibians and reptiles in colour. Collins, Auckland

Romijn RL (2007) Predation by the southern bell frog (*Litoria raniformis*) on the common skink (*Oligosoma nigriplantare polychroma*) in New Zealand. Herpetofauna 37:104–107

S[mith] WW (1884) *Sceloglaux albifacies* (laughing owl). N Z J Sci 2:86–88

Shah B, Shine R, Hudson S, Kearney M (2003) Sociality in lizards: why do thick-tailed geckos (*Nephrurus milii*) aggregate? Behaviour 140:1039–1052

Shine R, Olsson MM, LeMaster MP, Moore LT, Mason RT (2000) Are snakes right-handed? Asymmetry in hemipenis size and usage in garter snakes (*Thamnophis sirtalis*). Behav Ecol 11:411–415

Somma LA (2003) Parental behaviour in Lepidosaurian and Testudinian Reptiles. Krieger Publishing, Malabar, FL

Southey IC (1985) The ecology of three rare skinks on Middle Islands, Mercury Islands. Unpublished MSc thesis, University of Auckland, Auckland

Spencer NJ, Thomas BW, Mason RF, Dugdale JS (1998) Diet and life history variation in the sympatric lizards *Oligosoma nigriplantare polychroma* and *Oligosoma lineoocellatum*. N Z J Zool 25:457–463

Stanley MC (1998) Homing in the skink, *Oligosoma grande*, within fragmented habitat. J Herpetol 32:461–464

Stephenson B (2012a) Moko skink (*Oligosoma moco*) feeding from flowers of the coastal ngaio (*Myoporum laetum*). BioGecko 1:46

Stephenson B (2012b) Suter's skink (*Oligosoma suteri*) scavenging from a dolphin carcass. BioGecko 1:45

Stephenson GJ, Bartle JA, Connor T, Cooper R, Dare P, Middleton B (1966) Report on a visit to the Poor Knights Islands, December 1965–January 1966. Unpublished report to the Commissioner of Crown Lands, Auckland

Taylor R (1870) Te ika a maui; or, New Zealand and its inhabitants. Illustrating the origin, manners, customs, mythology, religion, rites, songs, proverbs, fables, and language of the Maori and Polynesian races in general; together with the geology, natural history, productions, and climates of the country, 2nd edn. William McIntosh and H. Ireson Jones, Wanganui, London and New Zealand

Thomas BW (1981) *Hoplodactylus rakiurae* n.sp. (Reptilia: Gekkonidae) from Stewart Island, New Zealand, and comments on the taxonomic status of *Heteropholis nebulosus* McCann. N Z J Zool 8:33–47

Thomas BW (1982) A review of the herpetofauna of southern New Zealand with some taxonomic considerations. Herpetofauna (Aust) 14:22–34

Thomas BW (1985) Observations on the Fiordland skink (*Leiolopisma acrinasum* Hardy). In: Grigg G, Shine R, Ehmann H (eds) Biology of Australasian frogs and reptiles. Royal Zoological Society of New South Wales, Mosman, NSW, pp 17–22

Thomas BW (1987) Some observations on predation and scavenging by the introduced wasps *Vespula germanica* and *V. vulgaris*. Weta 1987:59–61

Thompson MB (2000) *Oligosoma* spp. (New Zealand skinks). Predation. Herpetol Rev 31:175

Thompson MB, Daugherty CH, Cree A, French DC, Gillingham JC, Barwick RE (1992) Status and longevity of the tuatara, *Sphenodon guntheri*, and Duvaucel's gecko, *Hoplodactylus duvaucelii*, on North Brother Island, New Zealand. J R Soc N Z 22:123–130

Tingley R, Hitchmough RA, Chapple DG (2013) Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol Conserv 165:62–68

Tocher MD (1998) Skinks with altitude-saving Otago's high-country lizards. Forest Bird 290:30–33

Tocher MD (2003) The diet of grand skinks (*Oligosoma grande*) and Otago skinks (*Oligosoma otagense*) in Otago seral grasslands. N Z J Zool 30:243–257

Todd AC (2005) The social mating system of *Hoplodactylus maculatus*. N Z J Zool 32:251–262

Torr GA, Shine R (1994) An ethogram for the small scincid lizard *Lampropholis guichenoti*. Amphibia-Reptilia 15:21–34

Towns DR (1972) The reptiles of Red Mercury Island. Tane 18:95–105

Towns DR (1975) Ecology of the black shore skink, *Leiolopisma suteri* (Lacertilia: Scincidae), in boulder beach habitats. N Z J Zool 2:389–407

Towns DR (1996) Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific rat *Rattus exulans*. Pac Conserv Biol 2:286–292

Towns DR (1999) *Cyclodina* spp. skink recovery plan, Threatened species recovery plan 27. New Zealand Department of Conservation, Wellington

Towns DR, Daugherty CH (1994) Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation. N Z J Zool 21:325–339

Towns DR, Elliott GP (1996) Effects of habitat structure on distribution and abundance of lizards at Pukerua Bay, Wellington, New Zealand. N Z J Ecol 20:191–206

Towns DR, McFadden I (1993) Chevron skink recovery plan (*Leiolopisma homalonotum*), Threatened species recovery plan 5. New Zealand Department of Conservation, Wellington

Towns DR, Daugherty CH, Newman DG (1985) An overview of the ecological biogeography of the New Zealand lizards (Gekkonidae, Scincidae). In: Shine R, Ehmann H, Grigg G (eds) Biology of the Australasian frogs and reptiles. Royal Zoological Society of New South Wales, Mosman, NSW, pp 107–115

Towns DR, Neilson KA, Whitaker AH (2002) North Island Oligosoma spp. skink recovery plan, 2001–2012, Threatened species recovery plan 48. New Zealand Department of Conservation, Wellington

Towns DR, Atkinson IEA, Daugherty CH (2006) Have the harmful effects of introduced rats on islands been exaggerated? Biol Invasions 8:863–891

Towns DR, Hitchmough RA, Perrott J (2016) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? Chap. 11. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Traveset A, Sáez E (1997) Pollination of *Euphorbia dendroides* by lizards and insects: spatio-temporal variation in patterns of flower visitation. Oecologia 111:241–248

Uetz P, Hosek J (2016). The reptile database. http://www.reptile-database.org. Accessed 17 Apr 2016

van Winkel D (2008) Efficiency of techniques for post-translocation monitoring of the Duvaucel's gecko (*Hoplodactylus duvaucelii*) and evidence of native avian predation on lizards. Unpublished MSc thesis, Massey University, Auckland

Vitt LJ, Pianka ER, Cooper WE Jr, Schwenk K (2003) History and the global ecology of squamate reptiles. Am Nat 162:44–60

von Hugel A (1875) Letter to RB Sharpe. Ibis 17:389–394

Walls GY (1982) Provisional results from a study of the feeding ecology of the tuatara (*Sphenodon punctatus*) on Stephens Island. In: Newman DG (ed) New Zealand herpetology. New Zealand Wildlife Service Department of Internal Affairs, Occasional Publication No. 2, Wellington, pp 271–276

Wedding CJ (2007) Aspects of the impacts of mouse (*Mus musculus*) control on skinks in Auckland, New Zealand. Unpublished MSc thesis, Massey University, Auckland

Werner YL (1973) Auditory sensitivity and vocalizations in lizards (Reptilia: Gekkonoidea, Iguanidae, Pygopodidae and Scincidae), Proceedings of the meeting of the Zoological Society of Israel. Isr J Zool 22:204–205

Whitaker AH (1968) The lizards of the Poor Knights Islands, New Zealand. N Z J Sci 11:623–651

Whitaker AH (1970) Neuseelandische echsen. Aqua Terra 7:93–101

Whitaker AH (1972) Lizard predators. Pepeke 19:4–5

Whitaker AH (1982) Interim results from a study of *Hoplodactylus maculatus* (Boulenger) at Turakirae Head, Wellington. In: Newman DG (ed) New Zealand herpetology. Proceedings of a symposium held at Victoria University of Wellington, 29–31 Jan 1980, vol 2. New Zealand Wildlife Service Occasional Publication, Wellington, pp 363–374

Whitaker AH (1984) *Hoplodactylus kahutarae* n. sp. (Reptilia: Gekkonidae) from the Seaward Kaikoura Range, Marlborough, New Zealand. N Z J Zool 11:259–270

Whitaker AH (1985) A survey of lizards of the Mt Ida area, Otago, 12–22 Mar 1985. Unpublished report to New Zealand Wildlife Service, Wellington

Whitaker AH (1987) The roles of lizards in New Zealand plant reproductive strategies. N Z J Bot 25:315–328

Whitaker AH (1991). Research on the striped gecko, (*Hoplodactylus stephensi*), on Maud Island Pelorus Sound, Marlborough, 6–12 Mar 1991. Unpublished report for New Zealand Department of Conservation, Wellington

Whitaker AH (1998) Striped skink (*Oligosoma striatum*) recovery plan 1998–2003. Threatened species recovery plan No. 24. New Zealand Department of Conservation, Wellington

Whitaker AH, Tocher MD, Blair T (2002) Conservation of lizards in Otago conservancy. New Zealand Department of Conservation, Wellington

Wilkinson AS, Wilkinson A (1952) Kapiti bird sanctuary: a natural history of the island. Masterton Printing, Masterton

Woodward TE (1941) Some aspects of the anatomy of *Naultinus elegans*, Gray. Unpublished MSc thesis, University of Auckland, Auckland

Worthy TH (2016) A review of the fossil record of New Zealand lizards. Chap. 3. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Wotton DM, Drake DR, Powlesland RG, Ladley JJ (2016) The role of lizards as seed dispersers in New Zealand. J R Soc N Z 46:40–65

Chapter 7
Reproduction and Life History of New Zealand Lizards

Alison Cree and Kelly M. Hare

Abstract New Zealand lizard species are characterised by their high incidence of viviparity (99 % of taxa) and 'slow' life histories. Female geckos and skinks typically mate and begin vitellogenesis in autumn, store sperm over winter and ovulate in spring. Pregnancies usually last at least 3 months, but gestation length, which is temperature dependent, may reach 14 months in some geckos (especially nocturnally foraging species). Some female geckos and skinks reproduce less than annually. Male geckos and skinks exhibit spermiogenesis during summer and/or autumn, with prolonged or continuous spermatocytogenesis and no period of complete testicular regression. Several features (autumn mating with prolonged vitellogenesis, possibility of a secondary mating season in spring, prolonged pregnancies with sometimes less-than-annual reproduction in females) have parallels with Tasmanian and South American lizards from similarly cool climates. Parallels also exist with New Zealand's egg-laying tuatara (*Sphenodon punctatus*), including less-than-annual reproduction, prolonged embryonic development and continuous spermatocytogenesis. Compared with sympatric skinks, geckos from temperate zones in New Zealand appear distinctive in their ability to retain fully developed offspring in utero over winter, to begin vitellogenesis before pregnancy has ended and to maintain a stable size of the testes and abdominal fat bodies year-round. New Zealand lizards generally exhibit traits at the slow end of the life-history continuum for small-bodied lizards. In particular, New Zealand geckos are exceptionally long-lived (at least 3–5 decades in the wild in several species), and, with clutch sizes $\leq$2, have extremely low annual reproductive output. Some ideas for future research are presented.

Keywords Age at maturity • Annual reproductive output • Diplodactylidae • Gestation • Longevity • Scincidae • Sexual dimorphism • Spermatogenesis • Vitellogenesis

---

A. Cree (✉)
Department of Zoology, University of Otago, Dunedin, New Zealand
e-mail: alison.cree@otago.ac.nz

K.M. Hare
Centre for Biodiversity and Restoration Ecology, Victoria University of Wellington,
Wellington, New Zealand

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_7

7.1 Introduction

Reproduction and life history are fundamental to the ecology and evolution of lizards, and knowledge of these topics underpins successful conservation. A defining feature of New Zealand's endemic lizard fauna, which influences numerous aspects of reproduction and life history, is the very high incidence of viviparity[1] (live bearing). All of the 43 extant diplodactylid gecko taxa (described and proposed species), and all but one of the 61 extant skink taxa, are apparently viviparous. The percentage of viviparous taxa (99 %) is thus much higher than for extant lizard species worldwide (~19 %; Stewart and Blackburn 2015). Indeed, apart from two species in New Caledonia, New Zealand geckos are the only live-bearing members of the entire Gekkota (Bauer 2013). Although the difference is not as extreme for skinks, the incidence of viviparity in New Zealand (98 % of taxa) is high compared with estimates for Scincidae as a whole (~31–43 %; Blackburn 1982; Shai Meiri, Tel-Aviv University, pers. comm.).

A strongly supported explanation for the adaptive significance of viviparity among squamates is the 'maternal manipulation hypothesis' (MMH). This hypothesis states that by retaining developing embryos in utero, a female is able 'to provide better incubation conditions for her offspring' (see Shine 2014 for historical overview). Subsumed within the MMH is the 'cold climate hypothesis', which proposes that viviparity is adaptive in cold climates because it allows female reptiles to provide thermal regimes that favour successful embryonic development (Shine 2014). The high incidence of viviparity among New Zealand taxa and the thermoregulatory changes that occur during pregnancy for at least two species of geckos (*Woodworthia*; Rock et al. 2000) are consistent with these hypotheses.

We begin this chapter by discussing female reproduction, covering seasonal cycles, aspects of ovarian and oviducal function (including sperm storage, gestation and issues noted in captivity), followed by hormone cycles. We then briefly describe the male reproductive system, covering anatomy, function and seasonal cycles. Next, we present information, including some new data, on sexual dimorphism in snout–vent length, and discuss aspects of life history, including clutch size, annual reproductive output for females, age at maturity and longevity. For each section, our approach is to discuss geckos first and then skinks. In the final sections, we make comparisons with cool-climate lizards from other southern hemisphere regions and with New Zealand's only non-squamate lepidosaur, the tuatara (*Sphenodon punctatus*), and end with suggestions for further research. For a glossary of technical terms, see Table 7.1.

---

[1] An older term 'ovoviviparity' (associated with an incorrect idea that live-bearing lizards simply retained eggs in their oviducts until embryos 'hatched' at the time of birth) has been discarded (Stewart and Blackburn 2015). See section on uterine morphology and placentation later in this chapter.

Table 7.1 Glossary of technical terms as used in this chapter

Term	Definition
Androgens	Compounds involved in the development and maintenance of male characteristics (the main natural form in lizards being testosterone)
Annual reproductive output	Here, the number of offspring or eggs produced on average by an individual female per year (the product of mean clutch frequency and mean clutch size)
Arginine vasotocin	A hormone secreted by the neurohypophysial region of the pituitary gland; induces oviducal contractions and birth or oviposition
Atresia	Here, a process in which ovarian follicles that have aborted vitellogenesis are resorbed (hence, atretic follicle)
Chorioallantoic placenta	One of the main placental tissues of viviparous lizards; develops dorsally over the embryo; formed by apposition of the chorioallantoic membrane to the uterine epithelium
Cloaca	The chamber at the end of the digestive tract that also receives products from the reproductive and urinary systems; the final chamber before the vent
Clutch size	The number of eggs or live offspring produced by a female in a reproductive cycle (sometimes referred to as litter size in viviparous species)
Conceptus	The structure that develops during pregnancy from the fertilised egg cell, including the embryo, its extraembryonic membranes and yolk sac (plural = conceptuses)
Corpus luteum	A temporary endocrine structure formed from the remains of the ovarian follicle after ovulation (plural = corpora lutea); secretes the hormone progesterone
Corticosterone	A glucocorticosteroid hormone produced by the adrenal cortex; involved in regulation of energy balance, immune reactions and stress responses
Epididymis	The coiled anterior part of the duct system that transports sperm, leading from the testis to the vas deferens; produces secretions; and may also store sperm (plural = epididymides)
Follicular stasis	An ovarian abnormality in which a yolk-filled follicle fails to ovulate and may eventually become necrotic
Granulosa	A cell layer that surrounds each developing oocyte in the ovary; part of the ovarian follicle
Hemiclitoris	Female homologue of a hemipenis, seen in embryos (at least) of female lizards (plural = hemiclitorises or hemiclitorides)
Hemipenis	One of a pair of eversible sacs that form the penises of male squamates (plural = hemipenes)
In utero	Within the uterine region of the oviduct
Lecithotrophy	Form of embryonic nutrition in which yolk is the major source of nutrition (cf. placentotrophy)
Lepidosaur	A member of superorder Lepidosauria (i.e. squamates and rhynchocephalians)
Omphaloplacenta	One of the main placental tissues of viviparous lizards; develops ventrally; formed by apposition of part of the yolk sac to the uterine epithelium
Oocyte	Egg cell
Oestradiol	An ovarian steroid hormone that stimulates vitellogenesis and female maturation; a type of oestrogen (also spelt estradiol and estrogen, respectively)

(continued)

Table 7.1 (continued)

Term	Definition
Ovarian follicle	A sac comprising an oocyte surrounded by specialised cellular layers (granulosa and theca)
Oviduct	The duct transporting oocytes from the ovary and within which fertilisation and egg shelling or embryonic development occur; subdivisible into several regions, including the uterine tube, uterus and vagina
Oviparity	The egg-laying parity mode (hence, oviparous)
Oviposition	The action of laying eggs
Parturition	The action of giving birth to live young
Progesterone	A steroid hormone, produced in females by the corpora lutea; associated with pregnancy
Pyriform cell	A large, pear-shaped cell found in the granulosa of ovarian follicles during the previtellogenic stage; distinctive to female squamates
Renal sex segment	A secretory region of the kidney present in male squamates, but not in other reptiles
Rhynchocephalian	A member of order Rhynchocephalia (of which the only living member is the tuatara, *Sphenodon punctatus*)
Seminiferous tubules	Tubules within the testis within which spermatozoa are produced
Sexual size dimorphism	A difference between the sexes in some aspect of body size, such as snout–vent length
Spermatid	A cell at a late stage in the development of spermatozoa
Spermatocytogenesis	The production and development of spermatocytes, the cells that eventually become spermatids
Spermatogenesis	Sperm production
Spermiogenesis	The maturation of spermatids into spermatozoa
Squamate	A member of order Squamata, the group of reptiles that includes lizards and snakes
Testosterone	The steroid hormone produced by the testes and considered to be the main androgen in male lizards (also produced to some extent by the ovaries of females)
Vas deferens	The posterior part of the duct system that transports sperm, leading from the epididymis to the cloaca (plural = vasa deferentia)
Viviparity	A parity mode in which live offspring develop within the mother and are delivered as such, rather than as eggs (hence, viviparous)
Vitellogenesis	The manufacture of the yolk protein precursor, vitellogenin, at the liver, and its uptake by ovarian follicles

Definitions are from various sources, including Cree (2014)

7.2 Seasonal Reproductive Cycles in Female Lizards

Viviparous lizards of New Zealand have, at most, one reproductive cycle per year (Table 7.2), and all well-studied species appear to be lecithotrophic (yolk forms the major nutrient resource for embryonic development). Vitellogenesis (in which the yolk protein precursor, vitellogenin, is produced at the liver and absorbed by growing ovarian follicles) proceeds rapidly from late summer or autumn in most species. Enlarged vitellogenic follicles remain present over winter until ovulation in spring. Pregnancies, in which embryos develop in the uterine region of the two oviducts, typically last 3 months or more. The major variations on this basic sequence are in the seasons of mating and vitellogenesis, the duration and location of sperm storage, the duration of pregnancy and whether reproduction occurs annually or less frequently. Below we provide examples, with references, of the basic female cycle for three well-studied viviparous geckos and one skink from Otago (Fig. 7.1) and then discuss some variations.

7.2.1 Reproductive Cycles in Female Geckos

The most detailed description of female reproduction is for *Woodworthia* geckos near Alexandra, in Central Otago (MacAvoy 1976). The collection sites (c. 180–400 m asl) have a near-continental climate of hot summers and cold winters. Geckos in this study were probably *W.* 'Central Otago', and are referred to hereafter as such, but a few *W.* 'Cromwell' may have been included. Nonetheless, the cycle (defined by dissections and light microscopy) is clear-cut and likely to remain the definitive one given the high conservation status of most taxa (Hitchmough et al. 2016; Towns et al. 2016). Like many *Woodworthia* species, these geckos are nocturnal foragers that bask cryptically on sunny days (Jewell 2011); they also disappear into deep crevices over winter (MacAvoy 1976). Vitellogenesis in *W.* 'Central Otago' begins in late summer in follicles about 4 mm in diameter and is completed by ovulation in early spring, with follicles attaining a maximum diameter of ~9–10 mm (Figs. 7.1a and 7.2a; Table 7.2). By this time, spermatozoa (stored in the vaginal region of the oviduct from a previous mating) have moved up to a location just anterior to the uterus, where fertilisation probably takes place. During pregnancy, one embryo develops within each uterus over about 3–4 months. The offspring are born during early–late summer, and females mate soon afterwards. The cycle then begins again with vitellogenesis, indicating that females exhibit annual reproduction (MacAvoy 1976).

Female *W.* 'Otago large' at Macraes Flat in eastern Otago, a higher-elevation (c. 600 m asl) site with cooler summers, illustrate a remarkable variation on the cycle described above (Fig. 7.1b; Table 7.2; Cree 1994; Cree and Guillette 1995; note, this taxon is also known as *W.* 'Otago/Southland': Nielsen et al. 2011). The cycle has been established using nonterminal techniques, including abdominal palpation, supplemented by dissections. Palpation by trained researchers can discriminate vitellogenesis, early–mid pregnancy, late pregnancy and nonreproductive or post-partum

Table 7.2 Characteristics of female reproduction in New Zealand lizards

Species (location)	Approx. latitude, °S (& elevation in m)	Daily activity	SVL at maturity (mm)	Mean adult SVL (mm)	Age at sexual maturity (y)	Longevity in wild (y)	Mating (mo)	DVG (mo)	GL (mo)	Parturition (mo)	Reproductive frequency	Mean clutch size (and ARO)
Geckos												
Dactylocnemis 'Three Kings' (Three Kings Is, Northland)[a]	34° 10′ (≤295)	N (b)	77	87.8	ND	ND	ND	ND	ND	Feb–Apr?	10/13 (77 %) pregnant in summer; implies < once/y on average	2 (1.54)
Hoplodactylus duvaucelii (Northern islands; Poor Knights Is to Motukaha Is)[b]	35–37° (≤460)	N (b)	110	121.9	ND	ND (~*45c*)	ND	7	>12?	ND	31/55 (56 %) mature-sized museum specimens were reproductive; implies pregnant ~ once every 2 y; palpations of live females are consistent	2 (1.12)
Hoplodactylus duvaucelii (North Brother I, Marlborough)[c]	41° 07′ (≤79)	N (b)	95	109.0	7	50	ND	ND	>12?	ND	Probably < annual, given small size of embryos in January	2 (1–2?)
Naultinus elegans (Albany, Auckland)[d]	36° 43′ (~60)	D	63	68 (MD)	2	ND (*20c*)	Jul–Aug	3?	≥9?	Aug–Oct	100 % pregnant/season	ND (ND)
Naultinus gemmeus (Otago Peninsula, Otago)[e]	45° 50′ (40–90)	D	63	71.9	3	12 (*16c*)	Jul–Sep	5	7	Apr–May	55/56 (98 %) reproductive; implies almost always once/y	1.96 (1.92)
Naultinus grayii (Karikari Peninsula, Northland)[f]	35° 02′ (60)	D	~80	ND	1.3–1.4	ND	Jul–Aug	3?	≥4?	Mar	All pregnant in late summer; implies annual	2 (2)
Naultinus manukanus	40° 35′ (~260)	D	69	73.4	4	ND	ND	ND	ND	ND	24/34 (71.0 %) pregnant in 2003;	1.92 (1.35)

(Stephens I, Marlborough)[g]											implies < once/y. Similar result in 1978 (10/14; 71 %)	
Toropuku stephensi (Stephens I, Marlborough)[h]	40° 35′ (140–225)	N (b)	60	72.7	ND	16	ND	ND	ND	ND	7/21 (33 %) pregnant in summer; implies pregnant once every 3 y on average (pooled data for 1990 and 2002)	1.86 (0.62)
Woodworthia maculata (Turakirae Head, Wellington)[i]	41° 26′ (≤100)	N (b)	45	52.0	4	27 (*37c*)	Feb–Apr	9	4–6	Feb–Mar	90 % pregnant in summer (no sample size); implies annual in most	1.98 (1.78)
Woodworthia ‘Central Otago’ (Alexandra, Otago)[j]	45° 15′ (180–400)	N (b)	50	61.3	ND	ND	Jan–Feb	8	4	Dec–Jan	29/29 (100 %) pregnant in early summer; implies annual	2 (2)
Woodworthia ‘Otago large’ (Macraes Flat, Otago)[k]	45° 28′ (500–710)	N (b)	68	76.5	8	31	Feb	9	12–14	Oct–Dec	97/174 (56 %) in early–mid pregnancy in summers of 1991–1992 and 1992–1993; implies once every 2 y in most individuals	1.75 (0.98)
Skinks												
Oligosoma alani (Mercury Is, Waikato)[l]	36° 39′ (≤100)	N	111	134.7	5	11	ND	ND	ND	Apr	Annual reproduction inferred	3 (3)
Oligosoma fallai (Three Kings Is, Northland)[m]	34° 10′ (≤295)	D & N	93	119.3	ND	ND	ND	ND	ND	Feb–Apr?	7/12 (58 %) pregnant in summer; implies pregnant ~ once/2 y	4.5 (2.61)

(continued)

Table 7.2 (continued)

Species (location)	Approx. latitude, °S (& elevation in m)	Daily activity	SVL at maturity (mm)	Mean adult SVL (mm)	Age at sexual maturity (y)	Longevity in wild (y)	Mating (mo)	DVG (mo)	GL (mo)	Parturition (mo)	Reproductive frequency	Mean clutch size (and ARO)
Oligosoma grande (Macraes Flat, Otago)[n]	45° 27′ (~500)	D	78–81	94.5	3–5	23 (*30c*)	Feb–Mar	7	4–5	Feb–Mar	90 % reproductive per year (1991–1993); 79 % pregnant over summer (1996–2002)	1.85–2.4 (1.46–2.17)
Oligosoma maccanni (Kaitorete Spit, Canterbury)[o]	43° 50′ (<50)	D	49	54.5 (both sexes)	2–3	8	Autumn	~6	2.5–3	Dec–Feb	96 % pregnant in spring/summer	3.5 MD (3.36)
Oligosoma maccanni (Macraes Flat, Otago)[p]	45° 28′ (500–700)	D	49	60.9	3–4	ND	Mar	5–6	4–5	Jan–Feb	19/19 (100 %) pregnant during Oct–Dec, implying pregnant each year	2.8–3.7 (2.8–3.7)
Oligosoma ornatum (Mangere Mountain, Auckland)[q]	36° 57′ (≤107)	C (b)	60–61	70 (MD)	ND	ND (*13c*)	Mar and spring?	6	3–4	Jan–Feb	Annual reproduction	5 (5)
Oligosoma otagense (Macraes Flat, Otago)[r]	45° 27′ (~500)	D	101–106	112.3	4–6	21 (*44c*)	~March	7	4–5	Feb–Mar	90 % reproductive per year (1991–1993); 81 % pregnant over summer (1996–2002)	1.74–2.6 (1.41–2.34)
Oligosoma polychroma (Wellington)[s]	~41° 17′ (≤100)	D	54	61.7	1.75	~3–4 (*6c*)	Mar	~6	3	Jan	All but one pregnant early summer; annual reproduction inferred	5.13 in ovaries (~5)
Oligosoma suteri (Motutapu I, Auckland and Mercury Is, Waikato)[t]	36° 39–46′ (≤100)	N (b)	67–75	79–89	3	12	Oct–Nov	7	~2 in utero + 3 in nest	Hatch Mar–Apr	Annual reproduction inferred	3.7 (3.7)

Oligosoma whitakeri (Mercury Is, Waikato)[u]	36° 39′ (≤100)	N (b)	78	92.5	4	18 (~*45c*)	ND	ND	ND	Apr	Biennial reproduction inferred	2 (1)

Species are listed in alphabetical order, with different populations listed north to south. All are viviparous except *Oligosoma suteri*

Daily activity (foraging period): D = diurnal, C (b) = crepuscular, but also basks; N (b) = nocturnal, but also basks; D & N = day and night (sources include Jewell 2011); longevity (maximum known) is not always specific to sex or population; values in *italics*, followed by a c, indicate a longer record reported in captivity; mating (month) is inferred or seen; *DVG* duration of vitellogenesis, *GL* gestation length, *ARO* annual reproductive output (mean no. of offspring/female/y), *DOC* Department of Conservation, *MD* median, *mo* month, *ND* no data, *SVL* snout–vent length, *y* year

[a] Parrish and Gill (2003); [b] Cree (1994, pers. obs.), Christmas (1995), and D. Keall (pers. comm.); [c] Barwick (1982), Cree (1994, pers. obs.), and Wilson (2010); [d] Hitchmough (1979), Robinson (1985), and Anastasiadis and Whitaker (1987); [e] Wilson and Cree (2003), Scharf et al. (2015), and Carey Knox, EcoGecko Consultants (pers. comm.); [f] Hitchmough (1982); [g] Hare et al. (2007); [h] Hare and Cree (2005); [i] Whitaker (1982), Robinson (1985), Anastasiadis and Whitaker (1987), and Cree (1994); [j] Macavoy (1976), Cree (1994), Cree and Guillette (1995), Rock et al. (2000), and Rock and Cree (2003); [k] Robinson (1985); Cree (1994, pers. obs.), Cree and Guillette (1995), Sheehan (2002); Cree et al. (2003), and Sheehan et al. (2004); [l] Towns (1994); Towns and Ferreira (2001), Scharf et al. (2015), and K. Miller (pers. comm.); [m] Parrish and Gill (2003); [n] Cree (1994, pers. obs.), Eifler and Eifler (1999), Tocher (2009), Scharf et al. (2015), and A. Salt, DOC (pers. comm.); [o] Morris (1974), as *L. zelandica*; Freeman (1997), Lettink et al. (2008), and M. Lettink (pers. comm.); [p] Holmes and Cree (2006), Hare et al. (2009, 2012), Molinia et al. (2010), and Hare and Cree (2011); [q] Fawcett (1964a, b), Porter (1987), and Scharf et al. (2015); [r] Cree (1994, pers. obs.), Coddington and Cree (1997), Tocher (2009), Scharf et al. (2015), and A. Salt, DOC (pers. comm.); [s] Barwick (1959), Scharf et al. (2015), and R. Romijn (pers. comm.); [t] Towns (1975), Cree (1994), Towns and Ferreira (2001), and Miller et al. (2010); [u] Southey (1985), Towns (1994), Cree (1994), Towns and Ferreira (2001), D. Keall (pers. comm.)

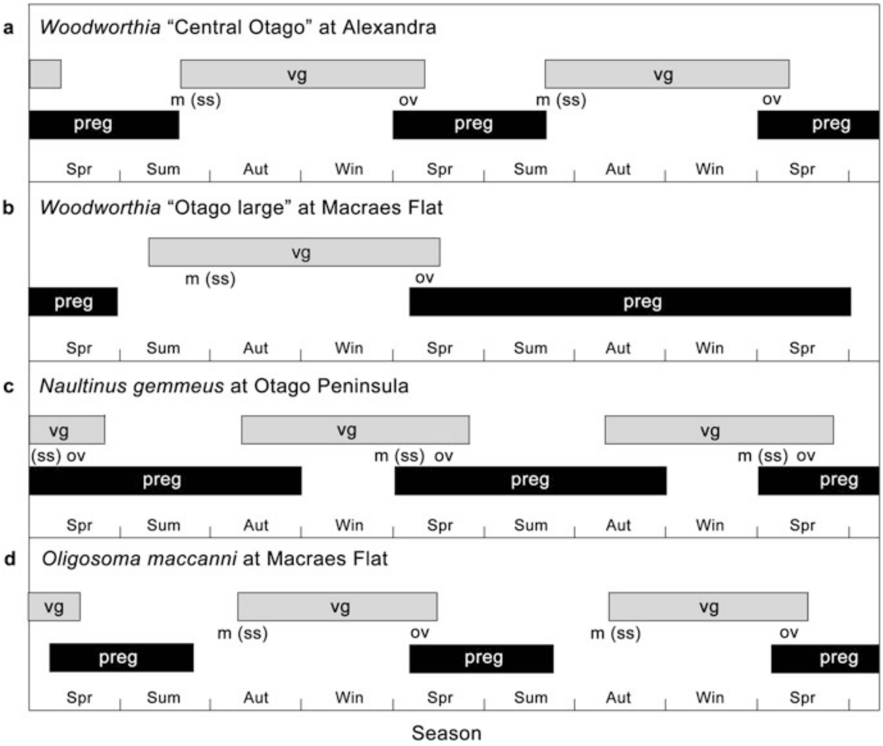


Fig. 7.1 Female reproductive cycles across 2 years for three representative gecko species and a skink from Otago. (**a**) *Woodworthia* 'Central Otago' at Alexandra [Data from MacAvoy ES (1976) The physiology of lizards from arid regions in Central Otago. Unpublished PhD thesis, University of Otago, Dunedin, New Zealand, with permission of Elizabeth MacAvoy]. (**b**) *W*. 'Otago/Southland' at Macraes Flat. [Modified from Wilson JL, Cree A (2003) Extended gestation with late-autumn births in a cool-climate, viviparous gecko from southern New Zealand (Reptilia: *Naultinus gemmeus*). Austral Ecology 28:339–348. Fig. 3. Copyright © 2003. Reprinted by permission of John Wiley & Sons.] [Additional data from Cree (pers. obs.) and Cree A, Guillette LJ, Jr (1995) Biennial reproduction with a 14-month pregnancy in the gecko *Hoplodactylus maculatus* from southern New Zealand. Journal of Herpetology 29:163–173. With permission of Society for the Study of Amphibians and Reptiles]. (**c**) *Naultinus gemmeus* at Otago Peninsula. [Modified from Wilson JL, Cree A (2003) Extended gestation with late-autumn births in a cool-climate, viviparous gecko from southern New Zealand (Reptilia: *Naultinus gemmeus*). Austral Ecology 28:339–348. Fig. 3. Copyright © 2003. Reprinted by permission of John Wiley & Sons.]. (**d**) *Oligosoma maccanni* at Macraes Flat. [Modified from Holmes KM, Cree A (2006) Annual reproduction in females of a viviparous skink (*Oligosoma maccanni*) in a subalpine environment. Journal of Herpetology 40:141–151. With permission of Society for the Study of Amphibians and Reptiles.] Note that (1) *W*. 'Otago large' at Macraes Flat requires 2 years to complete a reproductive cycle, whereas the three other species complete two cycles in the same time; (2) mating occurs during winter or spring in *N. gemmeus*, but during late summer or autumn in the other three species followed by a more prolonged period of sperm storage. *Grey bars* = vitellogenesis (vg); *black bars* = pregnancy (preg); m (ss) = mating followed by sperm storage; ov = ovulation

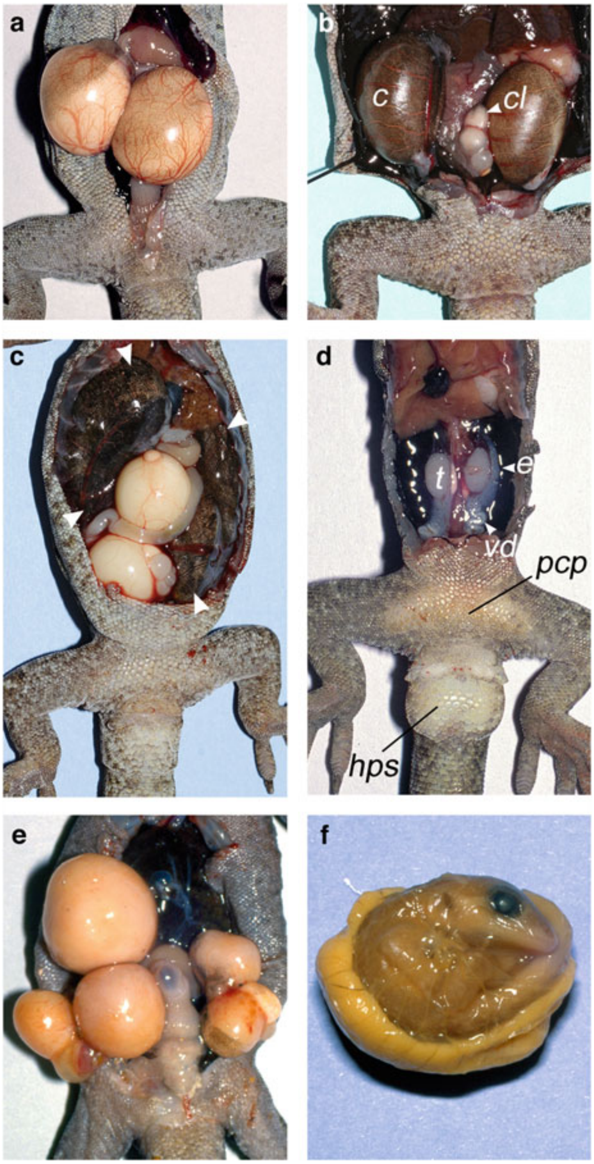


Fig. 7.2 Reproductive anatomy of New Zealand geckos. (**a**) *Female Woodworthia* 'Central Otago' in preovulatory condition in spring. (**b**) Female *W*. 'Otago large' in early pregnancy in spring. Note conceptus (*c*) in each of the two pigmented uteri. An active corpus luteum (*cl*, with stigma concealed) is visible at the anterior end of the left ovary, which also contains previtellogenic follicles. The right ovary is concealed. (**c**) Female *W*. 'Otago large' in late pregnancy (laboratory study). The two fully developed embryos (*white arrowheads denote margins*) and the ovaries (with enlarged vitellogenic follicles, corpora lutea and immature white previtellogenic follicles) fill most of the abdominal cavity. For a photograph of the same female with live neonates removed, see Cree and Hare (2010). (**d**) Male W. 'Otago large' in autumn. Note testis (*t*), epididymis (*e*), vas deferens (*vd*), precloacal pores (*pcp*) and hemipenial sac (*hps*) with spurs. (**e**) Female *Woodworthia* (unknown taxon from Otago) that was ailing in captivity. Note

(spent) conditions in this taxon (Wilson and Cree 2003). Vitellogenesis in *W*. ‘Otago large’ at Macraes Flat begins in midsummer, slightly earlier than at Alexandra (Cree and Guillette 1995). Mating occurs in late summer (Cree et al. 2003), and females store sperm over winter. Ovulation occurs in spring, soon after emergence from deep crevices (Fig. 7.2b). Embryos are fully developed, full size and viable by early autumn (Rock 2006; Rock and Cree 2008), but are retained in utero over winter and delivered in the following late spring/early summer (Cree and Guillette 1995; Rock 2006). Thus, pregnancy lasts up to 14 months (the longest recognised for any squamate; Stewart and Blackburn 2015), and most females appear to reproduce biennially (Cree and Guillette 1995; Cree et al. 2003; Penniket 2012). Such extended gestation is associated with cool summers; populations at higher elevations (c. 1039 m asl) also exhibit less-than-annual reproduction (Penniket 2012), whereas at most lower elevation sites (c. 50–450 m asl), annual reproduction is inferred since gestation is completed within one active season (Girling et al. 1997; Penniket 2012). Experimental studies with the Macraes Flat population confirm that gestation length is reduced with increased basking opportunity during pregnancy (Rock and Cree 2003; Cree and Hare 2010; Moore 2015). Further, the difference in gestation length between *W*. ‘Otago large’ and *W*. ‘Central Otago’ can be explained by differences in summer field temperatures, with no need to invoke population differences in genetics or body size (Cree and Guillette 1995; Rock and Cree 2003).

A third variation on seasonal cycles in female geckos is illustrated by *Naultinus gemmeus* on the Otago Peninsula (40–90 m asl; Fig. 7.1c; Table 7.2; Wilson and Cree 2003). This species forages diurnally and, unlike the two examples of *Woodworthia* above, continues to bask on sunny days during winter. Vitellogenesis occurs from autumn until spring, with follicles enlarging rapidly during late autumn (inferred from palpation). Mating has been reported (here or nearby) in winter and spring (Table 7.2), implying a short period of sperm storage compared with Otago populations of *Woodworthia*. Gestation lasts about 7 months, with parturition in late autumn. Vitellogenesis resumes almost immediately, allowing annual reproduction. Offspring are relatively large (10.0–12.3 % of maternal post-partum mass) compared with those of *W*. ‘Otago large’ (8.5–9.5 %; Rock 1999), which may assist survival over winter (Wilson and Cree 2003). At higher-elevation sites in Canterbury (c. 300–900 m asl), some female *N. gemmeus* appear to remain pregnant over winter, with reproduction possibly being less than annual for some individuals (Wilson and Cree 2003; Marieke Lettink, Fauna Finders, Christchurch, pers. comm.).

Among other *Woodworthia* geckos, an annual cycle with pregnancy lasting 4–6 months is well documented for *W. maculata* in coastal Wellington (Table 7.2) and the likely cycle for *W*. cf. *brunnea* in coastal Canterbury (McIvor 1972). Activity

---

Fig. 7.2 (continued) ovarian abnormalities including multiple hardened and aspherical follicles (atretic or in follicular stasis). (**f**) Conceptus of *Hoplodactylus duvaucelii* removed from the uterus in late pregnancy. The embryo (early stage 40, ~31 mm SVL) is still within its extraembryonic membranes, which, in combination with the uterine epithelium, form placental tissues. Photos © Alison Cree continues during winter and spring in *Naultinus* species other than *N. gemmeus*, with mating also occurring during these seasons (Table 7.2; Jewell 2011). However, at least in northern New Zealand, vitellogenesis appears restricted to spring (Hitchmough 1979). Limited evidence for *Naultinus* suggests ovulation late in spring or early summer, after a brief period of sperm storage (McCann 1955; Robinson 1985; Todd 2003). Although parturition occurs during late summer–early autumn in several *Naultinus* species (Table 7.2; Jewell 2011), *N. elegans* gives birth during winter or spring (Table 7.2); spring delivery (in captivity soon after collection) is also recorded for *Naultinus* in Hawke's Bay (Colenso 1880). Mating in both autumn and spring has been noted for *Mokopirirakau granulatus* (as *Hoplodactylus granulatus*) in captivity (Rowlands 1999).

New Zealand's largest gecko, *Hoplodactylus duvaucelii*, probably has less-than-annual reproduction in northern regions and Cook Strait populations, with pregnancies potentially lasting a year or more (Table 7.2). However, in captivity, pregnancies are apparently completed within a summer, following mating in spring (Rowlands 2000; Barry et al. 2010). Other geckos in which not all mature-sized females are pregnant in summer include *Dactylocnemis* 'Three Kings' (Parrish and Gill 2003), *Toropuku stephensi* on Stephens Island (Hare and Cree 2005), *Mokopirirakau kahutarae* at Kahutara Saddle (Cree & Whitaker pers. obs.) and *Tukutuku rakiurae* on Stewart Island (Whitaker 1994). In the latter species, the "very early stage of development" in embryos in late summer (Thomas 1981) suggests that pregnancies continue over winter. Pregnancies extending over winter also seem likely from the spring births reported for *M.* 'Roys Peak' (Jewell 2011).

7.2.2 Reproductive Cycles in Female Skinks

Among viviparous skinks, reproductive cycles described for diurnal *Oligosoma* are annual and broadly similar to that of *W.* 'Central Otago'. For example, *O. maccanni* at Macraes Flat reproduce annually (Fig. 7.1d; Table 7.2; Holmes and Cree 2006). Mating is inferred in early autumn (Molinia et al. 2010) and vitellogenesis begins by mid-autumn (Holmes and Cree 2006). Ovulation (at a follicle diameter of 5–7 mm) occurs in early spring, and pregnancies of about 4–5 months end during mid-to-late summer. Among females collected in late pregnancy from elevations of 564–719 m asl, births were delayed by about 8 days in those from the highest elevations compared with the lowest elevations (Hare and Cree 2011). When females are collected in early pregnancy, a laboratory regime with low basking opportunity slows gestation and leads to less successful pregnancies than under warmer regimes (embryonic development under the cool regime also appears less successful than in *W.* 'Otago large'; Cree and Hare 2010). Female offspring of *O. maccanni* produced under the cool regime were slower growing than those from warmer regimes, but offspring sex ratio was not affected by regime (Hare and Cree 2010).

Elsewhere in Otago, small-bodied *Oligosoma* at Alexandra (as *Leiolopisma zelandica*, probably including *O. maccanni*) ovulate in early spring (MacAvoy

1976). Parturition (after pregnancies of 3–4 months) occurs in early summer, and vitellogenesis begins in early autumn (both about a month earlier than at Macraes Flat). Sperm are stored for about 6 months in the vagina or uterus (MacAvoy 1976). In coastal Canterbury, female *O. maccanni* reproduce annually, with births peaking about a month earlier than at Macraes Flat (Table 7.2). Gestation may be as short as 2.5–3 months in this population (as *Leiolopisma zelandica*, but possibly a mixture of *O. maccanni*/*O. polychroma*: Morris 1974).

Other viviparous skinks with a similar annual cycle include *O. polychroma* from the South Island and lower North Island (Barwick 1959, as *L. zelandica*; Gill 1976, as *L.* sp.; Patterson and Daugherty 1990; Freeman 1997) and *O. ornatum* in Auckland (as *Sphenomorphus pseudornatus* in Fawcett 1964a, b; Porter 1987). Evidence implies both autumn and spring mating seasons for *O. ornatum* (Fawcett 1964a; Porter 1987). Unlike New Zealand geckos, no skinks are known to continue pregnancies over winter, although females of some nocturnally foraging species may reproduce less than annually (Table 7.2).

The nocturnally foraging *O. suteri*, New Zealand's only egg-laying lizard, reproduces annually. Vitellogenesis occurs from late autumn until mating and ovulation in mid–late spring, by which time ovarian follicles have grown to ~14 mm in diameter, with only a transient pause in growth during winter (Towns 1975). Embryos develop in the oviducts until oviposition in early summer (Towns 1975), when the development has reached ~ stage 32 of the 40-point scheme for *Zootoca vivipara* (Hare et al. 2002). The leathery-shelled eggs are ~14 mm long at oviposition (Towns 1975) and swell during development (Whitaker 1968). Clutch size of individual lizards (2–5 eggs: Towns 1975; Hare et al. 2002) is smaller than in some natural nest chambers (up to 11 eggs), suggesting communal nesting (Whitaker 1968). Nests are laid in sand or gravel under large stones on beaches (Whitaker 1968), where eggs incubate for 3 months, hatching in early autumn; thus, embryonic development takes 5 months (Towns 1975). Under laboratory conditions, mean incubation period increases from 52 days at 26 °C to 138 days at 18 °C; however, offspring from 18 °C were less likely to hatch, and those that did were smaller, had abnormalities, grew poorly and had reduced survival compared with those from warmer incubation temperatures (Hare et al. 2002, 2004). Both sexes were obtained from all three incubation temperatures, suggesting an absence of temperature-dependent sex determination (Hare et al. 2002; but see later section on sexual dimorphism at birth).

7.3 Growth and Vitellogenesis of Ovarian Follicles

The paired ovaries of New Zealand lizards are located in the posterior abdomen close to the dorsal body wall (Fig. 7.2a–c; Fig. 7.3c). A hierarchy of several follicles (each containing an oocyte) can be seen through the transparent ovarian epithelium. The small, white, previtellogenic follicles have the multilayered and polymorphic granulosa expected for squamates (Jones 2011), with small cells, intermediate cells and large pyriform cells (Fig. 7.4a; Boyd 1940; MacAvoy 1976). Enlarging follicles

Fig. 7.3 Reproductive anatomy of the New Zealand skink *Oligosoma maccanni*. (**a**) Cloacal region of female in early summer. Note the absence of hemipenes. (**b**) Cloacal region of male in early summer. Note vascularized bases of the hemipenes (not fully everted). (**c**) Female in early vitellogenesis in mid-autumn. The vitellogenic follicles (two in one ovary, one in the other) are about 3 mm in diameter. Note enlarged fat bodies (*f*). (**d**) Male in midsummer with a prolapsed cloaca. Note the large testis (*t*), the proximity of the vas deferens (*vd*) to the kidney (*k*), which contains a renal sex segment, and the presence of hemipenes, indicated by ridges with a depression between them at the base of the tail. (**e**) Female in mid-pregnancy in early summer. Two developing conceptuses (*c*) are present. One oviduct also contains a nondeveloping yolk mass (*white arrowhead*). (**f**) Female with three conceptuses in late pregnancy in midsummer. Note that embryos (located on the dorsal surface of conceptuses) are concealed by yolk in (**e**) and (**f**). Photos © Alison Cree. See also Holmes (2004)

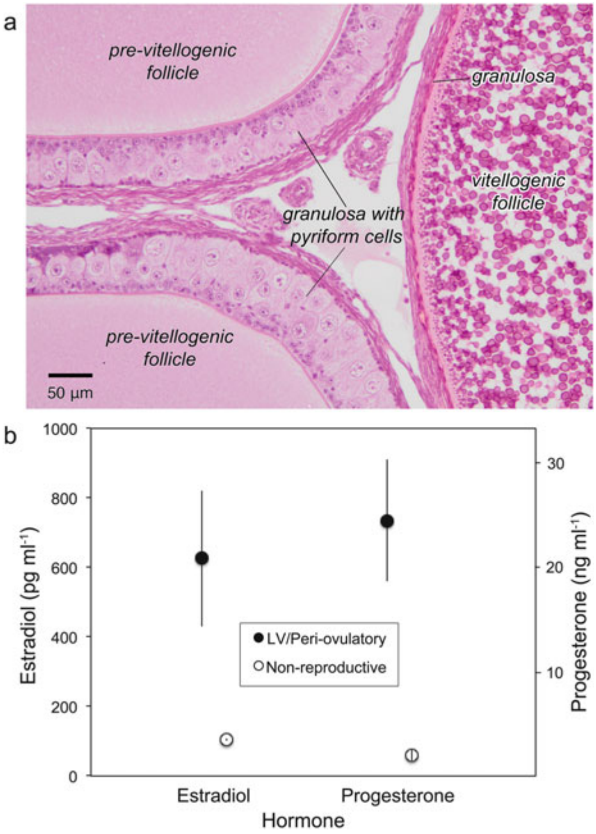


Fig. 7.4 Ovarian histology and plasma hormone concentrations in female geckos. (**a**) Light microscopy of ovarian follicles in *Woodworthia* 'Otago large'. As in all squamates, the previtellogenic follicles exhibit a multilayered granulosa containing small, intermediate and large (pyriform) cells. The enlarged vitellogenic follicle to the right contains yolk granules within the oocyte cytoplasm and a single-layered, monomorphic granulosa. (**b**) Mean plasma oestradiol and progesterone concentrations during spring (October) in female *Hoplodactylus duvaucelii*, a species in which not all females reproduce each year. Adult females were sampled on Lady Alice and Whatupuke Islands during early October 1993. Blood samples (withdrawn from the tail within 14 min of capture) were analysed using radioimmunoassays validated for tuatara (Cree et al. 1990). Females in late vitellogenesis (LV) or peri-ovulatory condition ($n = 10$) have much higher oestradiol and progesterone concentrations than nonreproductive females ($n = 5$; t-test, $p \leq 0.004$; Cree and Tyrrell unpublished). Bars for SE fall within the symbols for mean values in nonreproductive females

become cream and then yellow as vitellogenesis begins. Pre-ovulatory follicles are intensely yellow and highly vascularised (Fig. 7.2a).

Vitellogenesis is an energetically demanding process. In *W*. 'Central Otago' from Alexandra, stored fats in the tail and carcass may be more important in sustaining vitellogenesis than abdominal fat bodies, which show little seasonal size variation (mean mass remains between 0.3 and 0.7 % of body mass; MacAvoy

1976). In contrast, in *Oligosoma* from the same location, abdominal fat bodies reach a large mass relative to body mass by mid–late autumn (4.0 %), declining about 20-fold by late spring (to 0.2 %), and their stored fats (plus those from the tail) probably aid vitellogenesis (MacAvoy 1976). At Macraes Flat, abdominal fat bodies in female *O. maccanni* show a similar, though less dramatic, seasonal tendency to that in *Oligosoma* at Alexandra (Holmes and Cree 2006), as do those in female *O. suteri* on northern islands (Towns 1975). However, two small skinks from the North Island show a different seasonal pattern: the fat bodies are large in spring and become smaller during summer pregnancies (*O. polychroma*: Barwick 1959; *O. ornatum*: Fawcett 1964a).

Atretic follicles (those that are degenerating and being resorbed prior to ovulation) appear uncommon in New Zealand geckos and skinks, at least in the wild (Boyd 1940; Barwick 1959; Fawcett 1964a; MacAvoy 1976; Holmes and Cree 2006). However, captive *Woodworthia* (particularly overweight individuals) sometimes recruit more than one vitellogenic follicle per ovary; the enlarged follicles often have an unhealthy appearance with signs of atresia (Fig. 7.2e), and some may enter follicular stasis (a condition in which mature, unovulated follicles eventually become necrotic; Rivera 2008). Museum specimens of *N. gemmeus* can contain more than one vitellogenic follicle per ovary, sometimes with macroscopic signs of atresia in the smaller follicle (Wilson and Cree 2003). In a captive *H. duvaucelii* exhibiting preovulatory stasis, the largest follicle reached a massive 32.5 mm in diameter and 10.2 g (in a female of 65 g); the ovaries were removed surgically, and the removed masses (yolk granulomas) were positive for the bacterium, *Salmonella enterica* (Le Souëf et al. 2015).

An intriguing feature of some New Zealand geckos is the ability to resume a substantial amount of vitellogenesis (with follicles reaching almost ovulatory size) before the end of pregnancy. This ability is rare, if not unique, among viviparous lizards and may be limited to the species and period during which fully developed embryos are carried in utero (Rock and Cree 2003; Cree and Hare 2010). This feature has been confirmed by dissection in captivity in *Woodworthia* (Fig. 7.2c; Cree and Hare 2010) and in a museum specimen of *N. gemmeus* (Wilson and Cree 2003). It has also been inferred from palpation in spring of some wild females of *N. gemmeus* at high-elevation sites, where it offers potential for annual reproduction in climates that might otherwise be marginal (Marieke Lettink, Fauna Finders, pers. comm.). This ability has not been observed in skinks.

7.4 Oviducts, Sperm Storage and Gestation

The paired oviducts of New Zealand lizards are positioned laterally in the abdomen (Fig. 7.2b). Three main regions are easily recognised (Boyd 1942; MacAvoy 1976; Todd 2003): a thin-walled and pleated anterior region, a wide and muscular uterus where embryonic development occurs and a short, sphincter-like vagina, which leads into the cloaca. In *W.* ‘Otago large’, the region anterior to the uterus has been subdivided histologically into the infundibulum, uterine tube and isthmus (Girling et al. 1997, 1998; Girling 2002).

As noted above, sperm storage appears common in female geckos, especially in *Woodworthia*. In *W*. 'Central Otago' and *W*. 'Otago large', sperm are abundant in the vaginal lumen after mating in late summer or autumn, and most have reached the storage glands of the posterior uterine tube about 6 months later in spring (MacAvoy 1976; Girling et al. 1997). Species of *Naultinus*, with winter or spring mating and spring ovulation, have a shorter period of sperm storage, for which the uterine tube may predominantly be used (Todd 2003). Stored sperm have not been detected in *H. duvaucelii* in late vitellogenesis (Girling et al. 1998); this species appears to ovulate very soon after mating in spring. Small-bodied *Oligosoma* from Alexandra store sperm in the vagina for about 6 months, with no specialised storage sites in the upper oviduct (MacAvoy 1976). Whether females of any species can retain viable sperm for use in a subsequent reproductive cycle is unknown.

Once fertilised, the ovulated egg (now called a conceptus, i.e. yolk, embryo and extraembryonic membranes) fills the entire uterine region in geckos (Fig. 7.2b). Although it has been suggested that 3–4 offspring may be produced by an individual gecko (McCann 1955), definitive evidence is lacking. In numerous studies on wild *Woodworthia*, more than one conceptus per uterus has never been observed (Boyd 1940, 1942; McIvor 1972; MacAvoy 1976; Robinson 1985; Cree pers. obs.), and it seems highly unlikely that each uterus could accommodate more than one normal-sized offspring. In skinks, the ovulated oocytes sometimes pass to the contralateral oviduct (Barwick 1959; Fawcett 1964a). If clutch size is small, incubation chambers may form around each conceptus, but in larger clutches, there is one continuous chamber per uterus (Barwick 1959; Fawcett 1964a; MacAvoy 1976).

Macroscopically, the pregnant uterus of *Woodworthia* has an unusually dark appearance, reflecting the presence of melanin in the outer layer (Fig. 7.2b; MacAvoy 1976; Girling et al. 1997, 1998; Todd 2003). Possibly the pigmentation (which obscures embryonic development) protects embryos from ultraviolet radiation during cryptic basking, as the black peritoneum may also do (see Porter 1967 for other lizards). In small-bodied *Oligosoma*, including *O. maccanni*, the oviduct is not pigmented (Fig. 7.3e, f; MacAvoy 1976).

Morphology of the oviducts in *W*. 'Otago large' during vitellogenesis and pregnancy has been further described using light, scanning and transmission microscopy (with some information for *H. duvaucelii* also; Girling et al. 1997; Girling et al. 1998). As is typical of viviparous lizards, the uteri of New Zealand geckos contain very few uterine mucosal (shell) glands when compared with egg-laying geckos from overseas (Girling et al. 1997, 1998; see also Boyd 1942; MacAvoy 1976). The glands that do exist are probably the source of the thin, fibrous shell membrane that is initially present in pregnant *Woodworthia* but which disappears early in development (Boyd 1940, 1942; MacAvoy 1976; Girling et al. 1997). In small-bodied *Oligosoma* from Alexandra, a shell membrane is also initially present; although it disappears above the dorsally located embryo, fragments remain in the ventral region until late in pregnancy (MacAvoy 1976).

As in most squamates (Stewart and Blackburn 2015), in *Woodworthia* and *Oligosoma*, each conceptus exhibits a yolk cleft/isolated yolk mass complex during development (Boyd 1942; MacAvoy 1976). Placentas form from the close apposition of extraembryonic membranes to the uterine lining (Fig. 7.2f). The chorioallantoic placenta, which develops above the embryo, has been classified as type (i) in the Weekes scheme for representatives of both genera (Boyd 1942; MacAvoy 1976). The extent of nutritional transfer through the chorioallantoic placenta is probably modest but not yet quantified; the complex placentotrophy described in some skinks overseas (Stewart and Blackburn 2015) is not known in New Zealand species. An omphaloplacenta develops on the ventral surface of the yolk sac in both *Woodworthia* and *Oligosoma*. Female geckos and skinks increase in body mass during pregnancy (Wilson and Cree 2003; Cree and Hare 2010; Hare et al. 2010), and at least part of this increase is attributable to the increase in conceptus mass (two- to threefold; MacAvoy 1976; Holmes and Cree 2006), much of which probably results from water uptake through the omphaloplacenta.

In the wild, ovulated oocytes of geckos and skinks occasionally fail to develop (Fig. 7.3e), perhaps through a lack of fertilisation (Wilson and Cree 2003; Holmes and Cree 2006) although embryonic development can also fail (Barwick 1959). In captivity, failed embryos can be delivered prematurely (abortions) or fully formed but dead (stillbirths) (Cree and Hare 2010; Hare et al. 2011). In *W*. 'Otago large' from Macraes Flat, fully developed embryos suspected of being 'over-gestated' and at risk of death in utero can sometimes be recovered alive by injection of the neurohypophysial hormone arginine vasotocin (AVT), which induces uterine contractions (Cree and Guillette 1991). However, some females fail to respond. The reason(s) why some females fail to deliver what appear to be viable offspring is unclear, but nonthermal factors are suspected (Cree and Hare 2010; Moore 2015). In the skink *O. maccanni*, the presence of ectoparasitic mites was linked with pregnancy failure (Hare et al. 2011; failure was not attributed to palpation, the method used to assess pregnancy status). In New Zealand lizards (as for all squamates; Stewart and Blackburn 2015), there is no definite evidence that abortive conceptuses can be resorbed; instead, these and stillbirths are extruded and sometimes eaten, resulting in distinctive black, smeared faeces in captive *O. maccanni* (Chamberlain et al. 2010; Hare and Cree 2011; Hare et al. 2011).

7.5 Hormone Cycles in Females

In lizards generally, oestradiol is produced by ovarian follicles during vitellogenesis (Jones 2011). Following ovulation of each oocyte, the follicular tissue remaining in the ovary collapses to form a corpus luteum. The corpora lutea are the source of progesterone during pregnancy (Jones 2011). In *Woodworthia* and small-bodied *Oligosoma*, corpora lutea decline in diameter during pregnancy and disappear within a few months after parturition (Boyd 1940; Barwick 1959; Fawcett 1964a; Robinson 1985; MacAvoy 1976; Holmes and Cree 2006).

Although the small size and/or rarity of most New Zealand lizards has hindered studies of plasma hormone cycles, some data are available. In *Hoplodactylus duvaucelii*, in which not all females begin pregnancy each spring (Table 7.2), hormone concentrations differ between groups of females. As expected, plasma concentrations of both oestradiol and progesterone during spring are significantly higher in females assessed (by palpation) as being in late vitellogenesis or periovulatory condition than in nonreproductive females (Fig. 7.4b). In female *W*. 'Otago large' at Macraes Flat, plasma progesterone concentrations are similarly elevated during the periovulatory period, remaining slightly elevated until mid-pregnancy (Cree pers. obs.). Plasma concentrations of corticosterone, an adrenal glucocorticosteroid with complicated roles in energy balance, immune reactions and the physiological stress response of reptiles do not appear to be affected by pregnancy in *H. duvaucelii* (Barry et al. 2010). Similarly, in female *W*. 'Otago large' at Macraes Flat, plasma corticosterone concentrations do not vary with reproductive condition, although they do vary with season (Girling and Cree 1995; Cree et al. 2003). The lack of increase in plasma corticosterone concentration during gestation in these geckos contrasts with the situation in some viviparous squamates, but few species have been studied to date (Tokarz and Summers 2011; see also discussion in Girling and Cree 1995).

Among New Zealand skinks, plasma progesterone is elevated from late vitellogenesis until late pregnancy in *O. maccanni*, with the highest concentration reached during mid-pregnancy (Holmes and Cree 2006). Plasma progesterone concentrations are also elevated in *O. otagense* and *O. grande* during pregnancy (Cree pers. obs.).

7.6 Reproductive Anatomy, Function and Seasonal Cycles in Males

7.6.1 Reproductive Anatomy and Function in Males

We begin by describing the reproductive anatomy of males to introduce terms necessary to interpret seasonal cycles. In both geckos and skinks, the creamy-grey-white testes are roughly ovoid in shape and lie in the posterior abdomen close to the dorsal body wall (Figs. 7.2d and 7.3d). Dorsolateral to each testis lies a compact, coiled system of tubules (the epididymis) through which spermatozoa (sperm) pass and receive secretions. Each epididymis transitions into a wider, straight-walled vas deferens, which passes over the ventral surface of the reddish-brown kidney before entering the cloaca. As in all male squamates (Gist 2011), a specialised region of the kidney, the renal sex segment, produces secretions that contribute to seminal fluid (MacAvoy 1976). Paired hemipenes are stored retracted and inverted in the base of the tail (Figs. 7.2d and 7.3b). During copulation, sperm pass along a surface groove of the everted hemipenis to enter the female's reproductive system (Todd 2003).

Among New Zealand geckos, mean volume of the testes relative to body size is generally smaller than expected when compared with a sample of 63 squamate species from other countries (Todd 2008). Given that other studies have linked testis size to greater promiscuity, these patterns suggest that levels of promiscuity may be lower for New Zealand geckos than for overseas squamates (Todd 2008). Male geckos also have secretory precloacal pores (Fig. 7.2d), which are not seen in skinks. Precloacal pores are continuous with femoral pores on the under surface of the thighs in *Woodworthia*, *Naultinus*, *Mokopirirakau*, *H. duvaucelii*, *Tukutuku rakiurae* and *Toropuku stephensi* (in which they extend almost to the knee), but the pores do not extend onto the thighs in *Dactylocnemis* spp. (Nielsen et al. 2011). Waxy secretions from the pores probably play a role in communication, but this has yet to be confirmed experimentally.

7.6.2 Seasonal Reproductive Cycles in Males

The best description of the seasonal reproductive cycle for males of any New Zealand gecko is that for *Woodworthia* 'Central Otago' (MacAvoy 1976). In terms of size, the testes show no seasonal variation: their combined mean mass remains between 0.3 and 0.5 % of body mass throughout the year. Internally, however, the testes and associated ducts show a seasonal cycle. When geckos emerge in spring, spermatocytogenesis (the production and development of spermatocytes) has reached the spermatid stage. Spermiogenesis (the transformation of spermatids into spermatozoa) begins in late spring, peaking over summer. By the time that spermiogenesis comes to an end in mid-autumn, the next wave of spermatocytogenesis is underway; thus, there is no period of complete testicular regression. Sperm pack the epididymis and vas deferens between late spring and mid–late autumn. The renal sex segment is secretory between midsummer and late autumn, as are the precloacal pores. The peak mating season is during summer and autumn (when sperm appear in the female's tract), but some sperm remain present in the vas deferens in spring, raising the possibility of a secondary mating season just prior to ovulation. As in females, the abdominal fat bodies of male *W.* 'Central Otago' are relatively small ($\leq 0.7\,\%$ of body mass) and do not show an obvious seasonal cycle (MacAvoy 1976).

The less detailed information available for other species of *Woodworthia* is broadly consistent with the patterns described above for *W.* 'Central Otago'. In particular, testicular histology reveals spermiogenesis during late spring until at least late summer and a new wave of spermatocytogenesis during late summer and/or autumn, in *W.* 'Otago large' at Macraes Flat (Rock et al. 2000; Fig. 7.5), *W.* cf. brunnea in coastal Canterbury (McIvor 1972) and *W. maculata* at Turakirae Head (Robinson 1985). Mean testis volume (corrected for snout–vent length) did not vary across 11 months of the year in *W.* cf. *brunnea* in coastal Canterbury

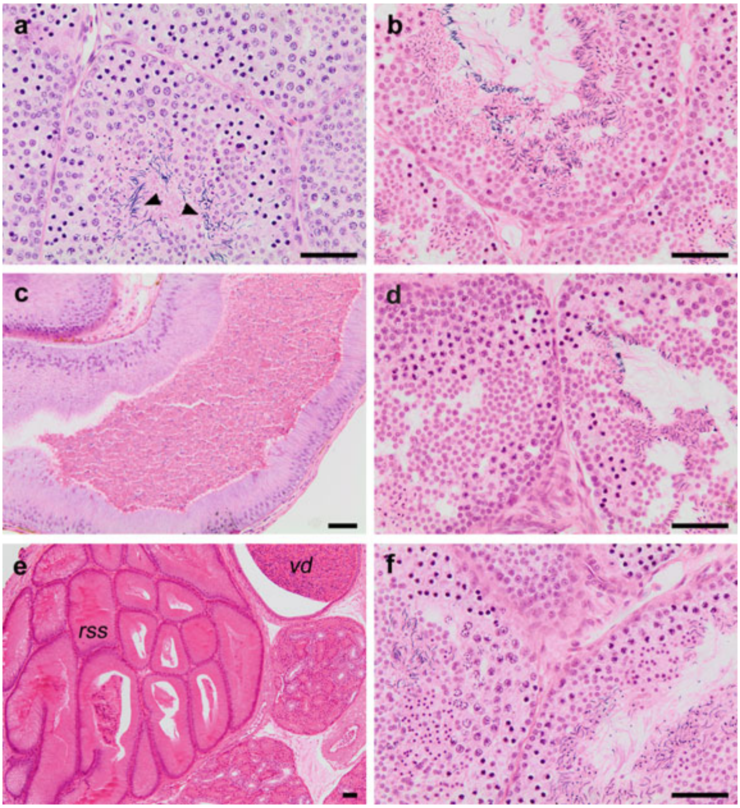


Fig. 7.5 Light microscopy illustrating seasonal reproduction in male *Woodworthia* 'Otago large' from Macraes Flat. (**a**) Testis in early spring (September), soon after emergence from deep crevices after winter. The lumens of the seminiferous tubules are closed, but spermatocytes are abundant, and initial stages of spermiogenesis, i.e. the transformation of spermatids (*black arrowheads*) into tailed spermatozoa, are apparent. (**b**) Testis in early summer (December). All stages of sperm development are present, including some mature spermatozoa in the lumens, which are now open. (**c**) Epididymal duct in midsummer (January). The epithelium is hypertrophied and secretory, and the duct is packed with sperm, secretions and cellular debris. (**d**) Testis in late summer (February). Proliferating spermatogonia and meiotically dividing spermatocytes are abundant. Spermiogenesis and spermiation have left deep crypts in the seminiferous epithelium in places. (**e**) Renal sex segment (*rss*) and vas deferens (*vd*) in the late summer mating season (February). The sex segment is hypertrophied and secretory, and the vas deferens is packed with sperm. (**f**) Testis in mid-autumn (April). All stages, including some residual spermatozoa, are present, though some lumens are closed. Animals will soon disappear into winter crevices. Scale bars are 50 μm in each. Photos © Alison Cree

(McIvor 1972) or in *W. maculata* at Turakirae Head (Todd 2008; see also Robinson 1985). As in *W.* 'Central Otago', sperm can be found in the epididymides or vasa deferentia of some male *W. maculata* in spring at Turakirae Head, supporting the possibility of a secondary mating season (Robinson 1985). There are intriguing suggestions of two sperm morphs (including a shorter, non-fertilising morph) in *W.* cf. *brunnea* (Todd 2008).

In *Naultinus* species, the limited evidence available indicates spermiogenesis, along with hypertrophy of the epididymis and renal sex segment, during late autumn and winter, shortly in advance of the winter–spring mating season (Robinson 1985). In *Dactylocnemis* 'Three Kings' from the subtropics, testicular size may reach a seasonal maximum in late summer (Parrish and Gill 2003), but information is sparse or lacking for other gecko species.

Among New Zealand skinks, the testes show greater seasonal variation in relative size and reach larger seasonal maxima relative to body mass, than those in New Zealand geckos (compare Figs. 7.3d and 7.2d). The seasonal cycle is best described for small-bodied *Oligosoma* from Alexandra, in which the testes varied in size from about 0.6 % of body mass (during autumn to spring) to about 3.7 % (in midsummer; MacAvoy 1976). Histologically, the seasonal cycle was similar to that in sympatric *W.* 'Central Otago'. Spermiogenesis was apparent from late spring until early autumn; a new wave of spermatocytogenesis was underway in autumn before the end of spermiogenesis. Sperm packed the epididymides and vasa deferentia during autumn (when the renal sex segments were also hypertrophied), and some sperm remained in the epididymides or vasa deferentia until late winter or spring (MacAvoy 1976). The mass of the abdominal fat bodies relative to body mass varied seasonally in males from 0.4 % in mid-spring to 2.3 % in midsummer, with a smaller summer peak and less dramatic decline over winter than observed in females (MacAvoy 1976).

Males of *O. polychroma* (as *L. zelandica*) from Wellington appear to have a similar annual cycle, although again the evidence is limited. Testicular mass was largest in late summer (when the epididymides also contained abundant sperm) and smallest in winter, with growth resuming by spring (Barwick 1959). In *O. suteri*, testis length was greatest in autumn and smallest in spring, with spermiogenesis evident by late spring; sperm were abundant in the epididymides from mid-autumn until midwinter (Towns 1975). Male *O. ornatum* (as *Sphenomorphus pseudornata*) may differ somewhat from the above patterns in that the testes appeared firm in late winter or spring, but flaccid by late summer (Fawcett 1964a). Sperm were abundant in the epididymides of *O. ornatum* in spring and summer, but absent in winter; the hemipenial area was swollen and 'purplish' in autumn and spring, suggesting that mating occurs in both seasons (Fawcett 1964a; Porter 1987).

7.7 Sexual Dimorphism

At birth, New Zealand lizards often show no distinguishing differences between the sexes. For example, among fully developed embryos or neonates of three gecko taxa (*W.* 'Otago large', *H. duvaucelii* and *D. pacificus*) and the skink *O. maccanni*, the hemipenes and hemiclitori are of similar size (Cree et al. 2004, 2007); only later in development do the hemipenes enlarge in males and the hemiclitori regress in females (Cree pers. obs.). This lack of obvious dimorphism in the genitalia contrasts with the situation in some lizards overseas; in many species, the presence vs absence of hemipenes at birth has been used to infer sex (e.g. Harlow 1996). Although initial research on the New Zealand skink *O. suteri* suggested that hemipenial eversion at birth (with histological support from a subset) could be used to assign sex (Hare et al. 2002), recaptures 5–7 years later of 21 individuals released to the wild showed that although eight had been correctly assigned as males, four of 13 had been incorrectly assigned as females (K. Hare pers. obs.). These results may indicate either difficulty in fully everting the hemipenes of neonates or incomplete sexual differentiation at birth.

As male geckos approach maturity, their sex becomes identifiable from the enlarging hemipenial sac that stores the hemipenes. ‘Spurs’ (formed from enlarged scales) are also present on each side of the sac (Fig. 7.2d). In larger males, the precloacal pores become obviously secretory, and the region surrounding them may take on a coloured ‘triangle’ (Fig. 7.2d; MacAvoy 1976). In adult males of *W.* ‘Otago large’ during the late-summer mating season, plasma concentrations of testosterone increase as snout–vent length increases (Cree et al. 2003). Evidence from lizards generally (Gist 2011) suggests that in addition to stimulating the reproductive tract and mating behaviour, the higher concentrations of plasma testosterone in larger males probably trigger increased secretory activity of the precloacal pores.

The morphological differences noted above, sometimes combined with data on reproductive condition of females, are often used for sex assignment in geckos of presumed adult size. Once sex is assigned, patterns of sexual size dimorphism (SSD) can be examined. Among lizards generally, SSD is highly labile among genera and even species, probably reflecting a balance between sexual selection towards large males and fecundity selection towards large females (Scharf and Meiri 2013; Cox and Kahrl 2015).

Our comparison of SSD in snout–vent length for New Zealand geckos (Table 7.3) is restricted to data sets where $n \geq 10$ per sex. We note, however, that larger sample sizes will have greater statistical power, that not all characteristics of ‘maleness’ necessarily confirm physiological maturity and that sexual dimorphism in the relative size of heads and abdomens may still exist even when no dimorphism in snout–vent length is detected (Scharf and Meiri 2013). Examined in this way, some gecko species or populations show no significant SSD in snout–vent length, some show female-larger dimorphism and some show male-larger dimorphism. Within the genus *Woodworthia*, all three patterns can be observed (Table 7.3). Furthermore, within *W.* ‘Otago large’, which is significantly female larger at Macraes Flat (Table 7.3), additional data show that the degree of sexual dimorphism in minimum snout–vent length at maturity increases significantly among populations as body size increases and as potential basking temperatures decrease (Penniket and Cree 2015). In other words, at cool sites (which tend to be at higher elevation and where geckos tend to be larger bodied), females mature at a larger size (by about 4–6 mm snout–vent length) than do males, whereas at warmer sites, geckos are smaller overall and there is little if any sexual difference. The variation

Table 7.3 Evidence for sexual size dimorphism in wild populations of some endemic New Zealand lizards

Species (location)	Female SVL			Male SVL			Significance	Source
	n	mean ± SE (mm)	max (mm)	*n*	mean ± SE (mm)	max (mm)		
Geckos								
Dactylocnemis 'Three Kings' (Three Kings Is, Northland)	24	87.8 ± 1.0	ND	21	87.4 ± 0.9	ND	Not significant	Parrish and Gill (2003); our calculation of SE
Hoplodactylus duvaucelii (Green I, Mercury Is, Waikato)	15	122.8 ± 1.2	133	16	**126.8 ± 1.2**	132	$\boldsymbol{t_{29} = 2.342, p = 0.026}$	J. Monks, unpublished data
Hoplodactylus duvaucelii (Korapuki I, Mercury Is, Waikato)	31	122.4 ± 1.0	134	28	123.3 ± 0.7	131	$t_{57} = 0.711, p = 0.480$	J. Monks, unpublished data
Hoplodactylus duvaucelii (Korapuki I, Mercury Is, Waikato)	54	121.0 ± 0.6	131	59	120.9 ± 0.7	135	$t_{111} = 0.078, p = 0.938$	D. van Winkel, unpublished data
Hoplodactylus duvaucelii (North Brother I, Marlborough)	60	109.0 ± 3.5	116	71	111.2 ± 4.2	119	$t_{129} = 0.394, p = 0.695$	Barwick (1982)
Naultinus gemmeus (Otago Peninsula, Otago)	37	**71.9 ± 0.5**	79	23	65.7 ± 1.4	77	$\boldsymbol{t_{27} = 4.267, p < 0.001}$	Wilson (1998); Wilson and Cree (2003)
Naultinus manukanus (Stephens I, Marlborough)	37	**73.4 ± 0.6**	81	18	68.9 ± 0.9	75	$\boldsymbol{p < 0.01}$	Hare et al. (2007)
Toropuku stephensi (Stephens I, Marlborough)	21	72.7 ± 1.1	81	23	74.0 ± 2.0	80	$t_{42} = 1.001, p = 0.322$	Hare and Cree (2005) (reanalysed with all females combined)
Woodworthia chrysosiretica (Mana I, Wellington)	11	67.5 ± 1.3	73	10	70.7 ± 1.6	79	$t_{19} = 1.549, p = 0.138$	Hare et al. (2007); K. Hare, unpublished data
Woodworthia maculata (Ohinauiti I, Waikato)	15	73.5 ± 0.7	78	14	**76.6 ± 0.8**	83	$\boldsymbol{t_{27} = 3.037, p = 0.005}$	J. Monks, unpublished data
Woodworthia maculata (Maud I, Marlborough)	35	64.8 ± 0.6	~71	14	**70.6 ± 0.9**	~77	$\boldsymbol{p < 0.0001}$	Kelly (2015)
Woodworthia maculata (Mana I, Wellington)	87	69.0 ± 0.7	81	43	**72.7 ± 0.7**	80	$\boldsymbol{p = 0.002}$	Hare and Hoare (2005)

(continued)

Table 7.3 (continued)

Species (location)	Female SVL			Male SVL			Significance	Source
	n	mean ± SE (mm)	max (mm)	n	mean ± SE (mm)	max (mm)		
Woodworthia maculata (North Brother I, Marlborough)	18	71.2 ± 0.7	78	12	**74.9 ± 0.9**	80	$\mathbf{t_{28} = 3.208,}$ $\mathbf{p = 0.003}$	J. Monks, unpublished data
Woodworthia maculata (Turakirae Head, Wellington)	158	49.8 ± 0.4	ND	107	**52.5 ± 0.5**	ND	$\mathbf{p < 0.001}$	Sheehan (2002) (raw data from Whitaker 1982); see also Fitness et al. (2011)
Woodworthia ‘Central Otago’ (Alexandra, Otago)	25	61.3 ± 0.7	67	21	60.9 ± 0.7	67	$p = 0.690$	Sheehan (2002)
Woodworthia ‘Otago large’ (Macraes Flat, Otago)	122	**76.5 ± 0.4**	87	81	75.0 ± 0.6	87	$\mathbf{p = 0.012}$	Sheehan (2002); H. Sheehan and A. Cree, unpublished data
Skinks								
Oligosoma alani (Mercury Is, Waikato)	19	134.7 ± 2.2	145	21	129.2 ± 2.1	150	$t_{38} = 1.820,$ $p = 0.077$	K. Miller, unpublished data (includes translocated individuals)
Oligosoma grande (Macraes Flat, Otago)	48	**89.4 ± 1.2**	105	46	86.3 ± 1.0	100	$\mathbf{t_{92} = 2.022,}$ $\mathbf{p = 0.046}$	DOC GAOS Recovery Programme (unpublished data collected 1991–1993)
Oligosoma grande (Macraes Flat, Otago)	41	**98.1 ± 0.8**	109	40	88.3 ± 1.4	101	$\mathbf{p < 0.001}$	Greer and Whitaker (2002) (data collected 1994–1995)
Oligosoma lineoocellatum (Matiu I, Wellington)	65	**94.9 ± 0.8**	105	17	82.1 ± 1.7	94	$\mathbf{t_{80} = 7.195,}$ $\mathbf{p < 0.001}$	M. Booth, ZEALANDIA Sanctuary, unpublished data
Oligosoma lineoocellatum (St Arnaud, Nelson)	61	**76.3 ± 0.9**	92	39	70.7 ± 0.7	78	$\mathbf{t_{96} = 4.460,}$ $\mathbf{p = 0.0001}$	Spencer et al. (1998)
Oligosoma maccanni (Macraes Flat, Otago)	117	**60.9 ± 0.5**	74	49	57.2 ± 0.6	67	$\mathbf{t_{164} = 3.611,}$ $\mathbf{p < 0.001}$	Hare et al. (2009)
Oligosoma macgregori (Mana I, Wellington)	30	**107.0 ± 1.2**	117	22	99.1 ± 1.3	111	$\mathbf{t_{50} = 4.398,}$ $\mathbf{p < 0.001}$	K. Hare, unpublished data
Oligosoma moco (Lady Alice I, Hen and Chickens Is, Northland)	37	62.0 ± 0.8	74	14	60.1 ± 1.1	70	$t_{49} = 1.287,$ $p = 0.204$	B. Barr, unpublished data

Oligosoma ornatum (Whatupuke I, Hen and Chickens Is, Northland)	16	**58.4 ± 0.7**	65	13	55.7 ± 0.4	60	$\boldsymbol{t_{27} = 3.154}$, $\boldsymbol{p = 0.004}$	L. Sullivan & B. Barr, unpublished data
Oligosoma ornatum (Wellington, Wellington)	18	70.4 ± 2.0	87	15	67.5 ± 1.4	79	$t_{31} = 1.163$, $p = 0.254$	Romijn (2013)
Oligosoma otagense (Macraes Flat, Otago)	33	112.3 ± 1.5	130	19	112.0 ± 2.5	148	$t_{50} = 0.122$, $p = 0.903$	DOC GAOS Recovery Programme (unpublished data collected 1991–1993)
Oligosoma polychroma (Wellington, Wellington)	35	**61.7 ± 0.8**	70	61	58.3 ± 0.7	75	$\boldsymbol{t_{94} = 3.123}$, $\boldsymbol{p = 0.002}$	R. Romijn, unpublished data
Oligosoma polychroma (St Arnaud, Nelson)	81	**56.7 ± 0.7**	67	32	51.7 ± 1.0	65	$\mathbf{t_{66} = 4.220}$, $\mathbf{p = 0.0001}$	Spencer et al. (1998)
Oligosoma smithi (Korapuki I, Mercury Is, Waikato)	20	64.7 ± 0.8	71	26	63.4 ± 0.6	70	$t_{44} = 1.477$, $p = 0.146$	Hare and Miller (2009)
Oligosoma suteri (oviparous) (Hen and Chickens Is, Northland)	31	77.5 ± 0.8	90	18	79.1 ± 1.3	91	$t_{47} = 1.104$, $p = 0.275$	B. Barr, unpublished data
Oligosoma suteri (Korapuki Is, Mercury Is, Waikato)	72	89.2 ± 1.0	104	73	**95.2 ± 0.8**	110	$\boldsymbol{t_{143} = 4.597}$, $\boldsymbol{p < 0.001}$	Miller et al. (2010) (translocated from Green I)
Oligosoma townsi (Lady Alice I, Hen and Chickens Is, Northland)	15	78.1 ± 2.3	87	18	79.1 ± 1.3	87	$t_{31} = 0.385$, $p = 0.703$	B. Barr, unpublished data
Oligosoma townsi (Whatupuke I, Hen and Chickens Is, Northland)	16	**79.6 ± 1.1**	89	11	74.7 ± 0.9	81	$\boldsymbol{t_{25} = 3.141}$, $\boldsymbol{p = 0.004}$	L. Sullivan and B. Barr, unpublished data
Oligosoma whitakeri (Mercury Is, Waikato)	27	93.3 ± 1.6	113	14	92.0 ± 0.9	96	$t_{39} = 0.555$, $p = 0.582$	K. Miller, unpublished data (includes translocated individuals)

Species are listed in alphabetical order, and populations within species are listed approximately north to south. All are viviparous except *Oligosoma suteri*. Populations in close proximity have been pooled where necessary to obtain sample sizes of at least ten for each sex. New statistical comparisons are reported in full (p values alone are from the source cited). Significant differences ($p < 0.05$) are shown in *bold*, with the mean for the larger sex also in *bold*

SVL snout–vent length, *ND* no data

in SSD observed among New Zealand geckos suggests that selection pressures vary in ways that enhance either male competitive advantage (e.g. courtship in captivity increases with male size; Todd 2005) or female reproduction (e.g. offspring size increases with female size; see next section).

As is common among lizards generally (Scharf and Meiri 2013; Cox and Kahrl 2015), male New Zealand geckos sometimes have larger heads, on average, than conspecific females. For example, head width (adjusted for snout–vent length) was significantly larger for male than female *W. maculata* from Turakirae Head (Sheehan 2002); however, in a smaller sample from Maud Island (analysed photographically), no sexual difference was detected (Kelly 2015). In a multivariate analysis of head size (length, width and depth) among museum specimens, head size was significantly larger for males than females in several species of *Woodworthi*a and in *D. pacificus*, but not in other geckos including *H. duvaucelii* and several species of *Naultinus* (Todd 2003). Sexual differences in colouration have been noted for species of the diurnally active *Naultinus* (Hitchmough 1982; Hare et al. 2007; Jewell 2011).

Among adult skinks, males are typically differentiated from females by the presence of hemipenes, which, even without eversion, produce subtle ridges with a depression between them in the base of the tail (Fig. 7.3d for *O. maccanni*; for *O. grande* and *O. otagense*: Coddington and Cree 1997). Following sex assignment (by this means and/or female palpation), females of at least seven viviparous species of skinks have significantly larger snout–vent lengths (which favours large clutch size; see next section) than in males. The oviparous *O. suteri* is the only New Zealand skink species in which males are known to be significantly larger (in one population, Table 7.3).

Adult females of both *O. maccanni* (Hare et al. 2011) and *O. otagense* (Connolly 2005) have longer trunks (between the axilla, or armpit, and groin) relative to snout–vent length than males, whereas males have wider heads than females. These differences are not apparent at birth in *O. maccanni*, but the greater head width is detectable at 3 months (Hare et al. 2011). Relatively broad heads have also been reported in male *O. polychroma* (Barwick 1959), and wider heads are probably common in males of many species. In some skink species, males have longer tails relative to snout–vent length than in females (*O. polychroma*: Spencer et al. 1998), but others show no dimorphism in tail length (*O. maccanni*: Hare et al. 2011; *O. otagense*: Connolly 2005). Sexual colour differences in skinks are generally modest or lacking. However, female *O. suteri* exhibit a bright orange ventrum from late vitellogenesis until ovulation, which fades to pink after ovulation; in contrast, the ventrum is grey green or cream yellow in males and in females at other times (Towns 1975).

7.8 Clutch Size and Annual Reproductive Output

We return now to clutch size (the number of offspring produced in a clutch or litter) as a contributing factor to life history. Among geckos, clutch size is typically two (occasionally one) in wild populations (Table 7.2). This limitation is not unique to New Zealand species; a clutch size ≤ 2 is a feature of gekkotans worldwide (Dunham et al. 1988). Variation in maternal snout–vent length does not influence clutch size in *W*. 'Otago large' (Cree and Guillette 1995), but larger mothers produce larger offspring (Rock and Cree 2003; Penniket and Cree 2015). In contrast, clutch size is more variable in skinks. Mean clutch sizes of 3–5 are typical (Table 7.2), though individual clutches of up to 10 are known (in *O. polychroma*: Patterson and Daugherty 1990). Within skink species, clutch size increases with female snout–vent length (*O. suteri*; Hare et al. 2002; *O. maccanni*; Holmes and Cree 2006), but offspring mass does not (*O. maccanni*: Holmes and Cree 2006). Clutch size in skinks can be underestimated by palpation when the clutch is large, especially in late pregnancy (Holmes and Cree 2006).

A consequence of both small clutch size and a tendency to less-than-annual reproduction is that many New Zealand gecko species have very small values (sometimes less than one) for annual reproductive output (the mean number of offspring per female per year; Table 7.2; Cree 1994). Viviparous New Zealand skinks have somewhat larger values (typically 2–4; Cree 1994).

7.9 Longevity and Age at Maturity

Among squamates generally, maturity is typically reached in <2 years (Mesquita et al. 2016). Modal longevity (in the wild or captivity) is 4–6 years, with only about 3 % of species living more than 30 years (Scharf et al. 2015). Given that longevity is associated with infrequent reproduction, higher latitudes and cooler body temperatures (Scharf et al. 2015), it is not surprising that New Zealand lizards exhibit high values for age at maturity and longevity (for information confirming cool body temperatures, see Hare and Cree 2016). However, longevity among lepidosaurs is also associated with body mass (Scharf et al. 2015); yet, despite being small bodied, New Zealand lizard species (especially geckos) have exceptionally long lifespans.

Most New Zealand geckos take between 2 and 8 years to reach maturity. Not surprisingly, the slowest to mature (and the longest lived) tend to be the larger-bodied nocturnal foragers (Table 7.2). For example, *H. duvaucelii* on North Brother Island takes 7 years to mature and can live an estimated 50 years, and *W*. 'Otago large' at Macraes Flat, females of which take 8 years to mature, can live an estimated 31 years (Table 7.2). The latter value reflects the length of study, and greater values may yet be detected. To date, the record for longevity in the wild goes to *W*. cf. *brunnea* on Motunau Island, a small lizard (≤ 81 mm snout–vent length) for which the latest estimates of lifespan reach 53 years (Marieke Lettink, Fauna Finders, pers. comm.; see also Lettink and Whitaker 2006). The diurnally active *Naultinus* species appear to mature more rapidly (within about 2–4 years) and may live more than a decade (Table 7.2), but longevity is not well established for wild populations.

Among diurnal skinks, small-bodied *Oligosoma* mature within about 2–4 years and may live up to 8 years in the wild (Table 7.2). The larger-bodied species *O. grande* and *O. otagense* mature more slowly (in 3–5 and 4–6 years, respectively) and are capable of living 21–23 years in the wild (Table 7.2). Similar values have been estimated for the nocturnally foraging *O. whitakeri* (Table 7.2).

Data from lizards in captivity (which generally yield estimates about 13 % greater than in the wild; Scharf et al. 2015) broadly support the above trends. For example, longevity in captivity may approach or exceed 40 years for several species, including *Woodworthia* sp. (as *Hoplodactylus maculatus*), *H. duvaucelii*, *N. rudis*, *N. stellatus*, *O. macgregori* and *O. whitakeri* (Dennis Keall, pers. comm.; Meads p. 393 in Newman 1982; Hare et al. 2007).

7.10 Comparisons with Other Cool-Climate Lizards from the Southern Hemisphere and with Tuatara

As discussed in the preceding sections, New Zealand lizards have some unusual features of reproduction and life history when compared with lizards generally. Here we summarise some of these features and make comparisons with other lepidosaurs from cool, southern landmasses.

Compared with the prevalent pattern for seasonal reproduction in temperate lizards (i.e. mate in spring and produce offspring in summer; Vitt 2015), female New Zealand lizards are unusual. Females of most species mate and begin vitellogenesis in late summer or autumn and store sperm for many months over winter before ovulation (and a possible secondary mating season) in spring. Furthermore, in some species not all females reproduce each year. However, these patterns are not unique among small-bodied lizards, occurring also in some cool-climate species from Tasmania, Australia (Jones et al. 1997; Olsson and Shine 1999). Less-than-annual reproduction, with prolonged vitellogenesis including the winter months, has also been reported for some South American species (Ibargüengoytía and Cussac 1996).

Compared with the norm for gestation length in viviparous lizards (about 2–4 months), pregnancies in New Zealand lizards are often longer and, in some geckos, reach the upper limit (14 months) known for squamates (Stewart and Blackburn 2015). These extended pregnancies appear most likely in large-bodied, nocturnally foraging geckos, especially those from high latitudes and/or high elevations; however, such extended pregnancies may also occur in some *Naultinus* populations. Extended pregnancy with maintenance of fully developed offspring in utero over winter has not been observed in New Zealand skinks (which, based on limited research, seem less tolerant of cool maternal regimes during pregnancy). However, pregnancies of a year or more, with fully developed embryos maintained in utero over winter, are known for some species of *Niveoscincus* in alpine regions of Tasmania (Olsson and Shine 1999). Thus, the phenomenon is not unknown among skinks generally. New Zealand geckos may, however, be unique among viviparous squamates in their ability to undergo a substantial amount of vitellogenesis before pregnancy ends, allowing an overlap of reproductive cycles under climates that are marginal for annual reproduction (Wilson and Cree 2003).

As a consequence of their small clutch size and infrequent reproduction, New Zealand geckos have low values for annual reproductive output compared with oviparous geckos generally (Cree 1994). However, comparable values have been estimated for the oviparous species *Homonota darwini*, which inhabits a cold Patagonian climate and does not reproduce each year (Ibargüengoytía and Casalins 2007). In New Zealand skinks, annual reproductive output (typically 2–4) is not dissimilar to values for viviparous skinks of similar body size elsewhere in the world (Cree 1994).

New Zealand lizards have evolved for tens of millions of years in the same environment as tuatara (*Sphenodon punctatus*). Tuatara are the only living representatives of Rhynchocephalia, the sister group to squamates. Although the squamate and rhynchocephalian lineages separated about 250 mya and the oviparous tuatara is much larger than New Zealand lizards (up to c. 0.5–1 kg for females and males, respectively), living members of the two groups share features of slow life history, including a protracted duration of reproductive processes (Cree 2014, 2015). Parallels are particularly strong between tuatara and geckos that forage nocturnally. For example, female tuatara reproduce less than annually, vitellogenesis is prolonged and embryonic development (in the soil, for a year or more) takes a similar length of time to gestation in some New Zealand geckos.

Males of tuatara and New Zealand lizards also share some parallels. Spermiogenesis and mating often occur in late summer or autumn; spermatocytogenesis is essentially continuous (an unusual feature for temperate-zone reptiles, in which the testes are often quiescent during the cooler months; Gribbins 2011), and as in some geckos, there is no seasonal variation in testicular size (Saint Girons and Newman 1987; Cree 2014, 2015). Wild tuatara are also extremely long-lived (up to about a century; Cree 2014). Diurnal skinks show greater fluctuations in size of the testes than in geckos or tuatara and in size of the abdominal fat bodies than in geckos (the latter are entirely absent in tuatara), as well as less extreme (though still impressive) longevity. These differences correspond with indications of greater specialisation in the thermal biology of skinks than in geckos (Hare and Cree 2016) or tuatara (Cree 2014).

7.11 Conclusions and Ideas for Future Research

Information on reproduction and life history helps us understand the evolutionary history of different lineages. It is also increasingly valuable to conservation management. For example, information on reproductive processes and/or life-history traits contributes to assessments of species' vulnerability to decline (Tingley et al. 2013); to development of new approaches to manipulate reproduction, such as artificial insemination (Molinia et al. 2010); to producing offspring in captivity with suitable phenotypes for release to the wild (Hare et al. 2002, 2012); and to monitoring the success of translocations (Towns and Ferreira 2001).

To improve our understanding of evolutionary processes and to contribute more effectively to conservation, we recommend the following. First, more detailed information is needed on seasonal reproductive cycles, especially for nocturnally foraging skinks, for northern *Naultinus* species and for geckos and skinks generally from alpine and high-latitude areas. Such studies may help resolve questions such as whether any New Zealand skinks maintain pregnancies over winter. New imaging techniques, along with non-invasive hormone assessments, may hold value for such studies, as well as for exploring the phenomenon of simultaneous vitellogenesis and pregnancy in geckos and causes of atresia, follicular stasis and stillbirths in captivity. Ultrastructural studies of placental morphology and the extent of placental nutrient transfer would be of evolutionary interest, as would broader studies comparing suites of life history and physiological characters between geckos and skinks generally.

For lizards worldwide, studies of complex forms of parental care are in their infancy, though examples of such care are growing in number (While et al. 2015). Among *Woodworthia* species, social aggregations, involving juveniles and adult females in particular, are well known (Hare and Hoare 2005; Bauer 2013; Cree pers. obs.), and there is also an intriguing report of social assistance (Hoare and Nelson 2006). However, details of social structure, kin relationships and mating systems are essentially unknown for New Zealand lizards. Given the investment made by New Zealand geckos into few, relatively large offspring at infrequent intervals, it would not be surprising if these species, in particular, had evolved some level of parental care during the postnatal period. A closer study of these, and long-lived skinks, is recommended.

Acknowledgements Grateful thanks to Elizabeth MacAvoy and Rod Hitchmough for permission to cite their respective PhD and MSc theses; to Rod Hitchmough and David Chapple for taxonomic information; to Dennis Keall, Carey Knox, Marieke Lettink and Amanda Salt for unpublished observations; to Ben Barr, Matu Booth, Jackie Ludgate (née Wilson), Kim Miller, Jo Monks, Hugh Sheehan, Laurence Sullivan, Dylan van Winkel and the Department of Conservation's Grand and Otago Skink Programme for permission to include unpublished snout–vent length data; to Matthew Downes, the late Gerald Stokes, Jane Girling and undergraduate students for histological assistance; to Ken Miller for graphical assistance; to Daniel Blackburn and Shai Meiri for information regarding viviparity; to Susan Jones for comments on the MS; and to the Department of Psychology, University of Otago, for writing space for AC.

References

Anastasiadis JM, Whitaker AH (1987) Longevity of free-living *Hoplodactylus maculatus* (Reptilia: Gekkonidae). N Z J Ecol 10:141–142

Barry M, Cockrem JF, Brunton DH (2010) Seasonal variation in plasma corticosterone concentrations in wild and captive adult Duvaucel's geckos (*Hoplodactylus duvaucelii*) in New Zealand. Aust J Zool 58:234–242

Barwick RE (1959) The life history of the common New Zealand skink *Leiolopisma zelandica* (Gray, 1843). Trans R Soc N Z 86:331–380

Barwick RE (1982) The growth and ecology of the gecko *Hoplodactylus duvauceli* at The Brothers islands. In: Newman DG (ed) New Zealand herpetology. New Zealand Wildlife Service Occasional Publication No. 2, Department of Internal Affairs, Wellington, pp 377–391

Bauer AM (2013) Geckos: the animal answer guide. The Johns Hopkins University Press, Baltimore, MD

Blackburn DG (1982) Evolutionary origins of viviparity in the Reptilia. I. Sauria. Amphibia-Reptilia 3:185–205

Boyd MMM (1940) The structure of the ovary and the formation of the corpus luteum in *Hoplodactylus maculatus*, Gray. Quart J Microsc Sci 82:337–376 + plates pp 313–319

Boyd MMM (1942) The oviduct, foetal membranes and placentation in *Hoplodactylus maculatus* Gray. Proc Zool Soc London Ser A 112:65–104 + plate p 101

Chamberlain AJ, Cree A, Hare KM (2010) Mysterious moments: unveiling birth in a viviparous lizard. Proceedings of the second meeting of the Australasian Societies for Herpetology (Society for Research on Amphibians and Reptiles in New Zealand and the Australia Society for Herpetologists). N Z J Zool 37:65

Christmas E (1995) Interactions between Dauvaucel's gecko (*Hoplodactylus duvaucelii*) and kiore (*Rattus exulans*). Unpublished MSc thesis, University of Otago, Dunedin

Coddington EJ, Cree A (1997) Population numbers, response to weather, movements and management of the threatened New Zealand skinks *Oligosoma grande* and *O. otagense* in tussock grassland. Pac Conserv Biol 3:379–391

Colenso W (1880) Notes and observations on the animal economy and habits of one of our New Zealand lizards, supposed to be a new species of *Naultinus*. Trans N Z Inst 12:250–251

Connolly J (2005) A comparison of the "quality" of wild and captive Otago skinks (*Oligosoma otagense*): are captive stocks of potential use in conservation? Unpublished MSc thesis, University of Otago, Dunedin

Cox RM, Kahrl AF (2015) Sexual selection and sexual dimorphism. In: Rheubert JL, Siegel DS, Trauth SE (eds) Reproductive biology and phylogeny of lizards and tuatara. CRC Press, Taylor and Francis Group, Boca Raton, FL, pp 78–108

Cree A (1994) Low annual reproductive output in female reptiles from New Zealand. N Z J Zool 21:351–372

Cree A (2014) Tuatara: biology and conservation of a venerable survivor. Canterbury University Press, Christchurch

Cree A (2015) Reproductive anatomy and cycles of tuatara (*Sphenodon punctatus*), an intriguing non-squamate lepidosaur. In: Rheubert JL, Siegel DS, Trauth SE (eds) Reproductive biology and phylogeny of lizards and tuatara. CRC Press, Taylor and Francis Group, Boca Raton, FL, pp 620–646 + colour plate p 748

Cree A, Guillette LJ Jr (1991) Effect of β-adrenergic stimulation on uterine contractions induced by arginine vasotocin and prostaglandin $F_{2\alpha}$ in the gecko *Hoplodactylus maculatus*. Biol Reprod 47:499–510

Cree A, Guillette LJ Jr (1995) Biennial reproduction with a fourteen-month pregnancy in the gecko *Hoplodactylus maculatus* from southern New Zealand. J Herpetol 29:163–173

Cree A, Hare KM (2010) Equal thermal opportunity does not result in equal gestation length in a cool-climate skink and gecko. Herpetol Conserv Biol 5:271–282

Cree A, Guillette LJ Jr, Cockrem JF, Brown MA, Chambers GK (1990) Absence of circadian cycles in plasma concentrations of sex steroids in male and female tuatara (*Sphenodon punctatus*), and the effects of acute capture stress on females. Gen Comp Endocrinol 79:103–113

Cree A, Tyrrell CL, Preest MR, Thorburn D, Guillette LJ Jr (2003) Protecting embryos from stress: corticosterone effects and the corticosterone response to capture and confinement during pregnancy in a live-bearing lizard (*Hoplodactylus maculatus*). Gen Comp Endocrinol 134:316–329

Cree A, Rock J, Stokes G (2004) Sexual differentiation during embryonic and juvenile development in viviparous geckos (*Hoplodactylus* spp.). Proceedings of the 10th Biennial conference of the Society for Research on Amphibians and Reptiles in New Zealand. N Z J Zool 31:102

Cree A, Connolly J, Hare J, Holmes KM, Johnson G, Yeong C (2007) Reproductive studies on a non-threatened lizard (McCann's skink, *Oligosoma maccanni*): implications for the endangered skinks *O. grande* and *O. otagense* from southern New Zealand. Proceedings of the 12th Biennial conference of the Society for Research on Amphibians and Reptiles in New Zealand, University of Otago, Dunedin. N Z J Zool 34:262

Dunham AE, Miles DM, Reznick D (1988) Life history patterns in squamate reptiles. In: Gans C, Huey R (eds) Biology of the Reptilia, vol 16b. Alan R Liss, New York, pp 443–511

Eifler DA, Eifler MA (1999) Foraging behavior and spacing patterns of the lizard *Oligosoma grande*. J Herpetol 33:632–639

Fawcett JD (1964a) The life history and ecology of *Sphenomorphus pseudornatus* (McCann) (Lacertilia: Scincidae). Unpublished MSc thesis, University of Auckland, Auckland

Fawcett JD (1964b) The life history and ecology of *Sphenomorphus pseudornatus* (McCann). Bull Zool Dep Univ Auckl 1:25–26

Fitness J, Hitchmough RA, Morgan-Richards M (2011) Little and large: body size and genetic clines in a New Zealand gecko (*Woodworthia maculata*) along a coastal transect. Ecol Evol 2:273–285

Freeman AB (1997) Comparative ecology of two *Oligosoma* skinks in coastal Canterbury: a contrast with Central Otago. N Z J Ecol 21:153–160

Gill BJ (1976) Aspects of the ecology, morphology and taxonomy of two skinks (Reptilia, Lacertilia) in the coastal Manawatu area of New Zealand. N Z J Zool 3:141–157

Girling JE (2002) The reptilian oviduct: a review of structure and function and directions for future research. J Exp Zool 293:141–170

Girling JE, Cree A (1995) Plasma corticosterone levels are not significantly related to reproductive stage in female common geckos (*Hoplodactylus maculatus*). Gen Comp Endocrinol 100:273–281

Girling JE, Cree A, Guillette LJ Jr (1997) Oviductal structure in a viviparous New Zealand gecko, *Hoplodactylus maculatus*. J Morphol 234:51–68

Girling JE, Cree A, Guillette LJ Jr (1998) Oviducal structure in four species of gekkonid lizard differing in parity mode and eggshell structure. Reprod Fertil Dev 10:139–154

Gist DH (2011) Hormones and the sex ducts and sex accessory structures of reptiles. In: Norris DO, Lopez KH (eds) Hormones and reproduction of vertebrates, vol 3, Reptiles. Academic, London, pp 117–139

Greer AE, Whitaker AH (2002) The relationship between mass and snout-vent length in the New Zealand tor-inhabiting skink *Oligosoma grande*. Herpetol Rev 33:170–171

Gribbins KM (2011) Reptilian spermatogenesis: a histological and ultrastructural perspective. Spermatogenesis 1:250–269

Hare KM, Cree A (2005) Natural history of *Hoplodactylus stephensi* (Reptilia: Gekkonidae) on Stephens Island, Cook Strait, New Zealand. N Z J Ecol 29:137–142

Hare KM, Cree A (2010) Exploring the consequences of climate-induced changes in cloud cover on offspring of a cool-temperate viviparous lizard. Biol J Linn Soc 101:844–851

Hare KM, Cree A (2011) Maternal and environmental influences on reproductive success of a viviparous grassland lizard. N Z J Ecol 35:254–260

Hare KM, Cree A (2016) Thermal and metabolic physiology of New Zealand lizards. In: Chapple DG (ed) New Zealand lizards. Springer, Cham, pp 239–267

Hare K, Hoare JM (2005) *Hoplodactylus maculatus* (common gecko). Aggregations. Herpetol Rev 36:179

Hare KM, Miller KA (2009) What dives beneath: diving as a measure of performance in lizards. Herpetologica 65:227–236

Hare KM, Daugherty CH, Cree A (2002) Incubation regime affects juvenile morphology and hatching success, but not sex, of the oviparous lizard *Oligosoma suteri* (Lacertilia: Scincidae). N Z J Zool 29:221–229

Hare KM, Longson CG, Pledger S, Daugherty CH (2004) Size, growth, and survival are reduced at cool incubation temperatures in the temperate lizard *Oligosoma suteri* (Lacertilia: Scincidae). Copeia 2004:383–390

Hare KM, Hoare JM, Hitchmough RA (2007) Investigating natural population dynamics of *Naultinus manukanus* to inform conservation management of New Zealand's cryptic diurnal geckos. J Herpetol 41:81–93

Hare JR, Holmes KM, Wilson JL, Cree A (2009) Modelling exposure to selected temperature during pregnancy: the limitations of squamate viviparity in a cool-climate environment. Biol J Linn Soc 96:541–552

Hare KM, Hare JR, Cree A (2010) Parasites, but not palpation, are associated with pregnancy failure in a captive viviparous lizard. Herpetol Conserv Biol 5:563–570

Hare KM, Yeong C, Cree A (2011) Does gestational temperature or prenatal sex ratio influence development of sexual dimorphism in a viviparous skink? J Exp Zool A 315:215–221

Hare KM, Caldwell AJ, Cree A (2012) Effects of early postnatal environment on phenotype and survival of a lizard. Oecologia 168:639–649

Harlow PS (1996) A harmless technique for sexing hatchling lizards. Herpetol Rev 27:71–72

Hitchmough RA (1979) The ecology and behaviour of two green gecko (*Naultinus*) species. Unpublished MSc thesis, University of Auckland, Auckland

Hitchmough RA (1982) The ecology of a population of *Naultinus grayi* Bell near Kaitaia. In: Newman DG (ed) New Zealand herpetology. New Zealand Wildlife Service Occasional Publication No. 2, pp 399–407

Hitchmough R, Barr B, Monks J, Lettink M, Reardon J, Tocher M, van Winkel D, Rolfe J (2016) Conservation status of New Zealand reptiles, 2015, New Zealand Threat Classification Series. Department of Conservation, Wellington

Hoare JM, Nelson NJ (2006) *Hoplodactylus maculatus* (common gecko). Social assistance. Herpetol Rev 37:222–223

Holmes K (2004) The female reproductive cycle of a viviparous skink, *Oligosoma maccanni*, in a subalpine environment. Unpublished MSc thesis, University of Otago, Dunedin

Holmes KM, Cree A (2006) Annual reproduction in females of a viviparous skink (*Oligosoma maccanni*) in a subalpine environment. J Herpetol 40:141–151

Ibargüengoytía NR, Casalins LM (2007) Reproductive biology of the southernmost gecko *Homonota darwini:* convergent life-history patterns among southern hemisphere reptiles living in harsh environments. J Herpetol 41:72–80

Ibargüengoytía NR, Cussac VE (1996) Reproductive biology of the viviparous lizard, *Liolaemus pictus* (Tropiduridae): biennial female reproductive cycle? Herpetol J 6:137–143

Jewell T (2011) A photographic guide to reptiles and amphibians of New Zealand. Revised edn. Photographs by Rod Morris. New Holland Publishers, Auckland

Jones SM (2011) Hormonal regulation of ovarian function in reptiles. In: Norris DO, Lopez KH (eds) Hormones and reproduction of vertebrates, vol 3, Reptiles. Academic, London, pp 89–115

Jones SM, Wapstra E, Swain R (1997) Asynchronous male and female gonadal cycles and plasma steroid concentrations in a viviparous lizard, *Niveoscincus ocellatus* (Scincidae), from Tasmania. Gen Comp Endocrinol 108:271–281

Kelly CD (2015) Sexual size and shape dimorphism and allometric scaling patterns in head traits in the New Zealand common gecko *Woodworthia maculatus*. Zoology 118:248–254

Le Souëf AT, Barry M, Brunton DH, Jakob-Hoff R, Jackson B (2015) Ovariectomy as treatment for ovarian bacterial granulomas in a Duvaucel's gecko (*Hoplodactylus duvaucelii*). N Z Vet J 63:340–344

Lettink M, Whitaker T (2006) *Hoplodactylus maculatus* (common gecko): longevity. Herpetol Rev 37:223–224

Lettink M, Cree A, Norbury G, Seddon PJ (2008) Monitoring and restoration options for lizards on Kaitorete Spit, Canterbury, vol 301, Department of Conservation Research and Development Series. Department of Conservation, Wellington

MacAvoy ES (1976) The physiology of lizards from arid regions in Central Otago. Unpublished PhD thesis, University of Otago, Dunedin

McCann C (1955) The lizards of New Zealand: Gekkonidae and Scincidae. Dominion Museum Bulletin No. 17., Wellington

McIvor IR (1972) Ecology of a population of *Hoplodactylus pacificus*, the common New Zealand gecko (Reptilia: Gekkonidae). Unpublished MSc thesis, University of Canterbury, Christchurch

Mesquita DO, Faria RG, Colli GR, Vitt LJ, Pianka ER (2016) Lizard life-history strategies. Austral Ecol 41:1–5

Miller KA, Hare KM, Nelson NJ (2010) Do alternate escape tactics provide a means of compensation for impaired performance ability? Biol J Linn Soc 99:241–249

Molinia FC, Bell T, Norbury G, Cree A, Gleeson DM (2010) Assisted breeding of skinks or how to teach a lizard old tricks! Herpetol Conserv Biol 5:311–319

Moore G (2015) Thermal control of delivery date and resulting offspring condition in a viviparous gecko. Unpublished MSc thesis, University of Otago, Dunedin

Morris RW (1974) Some aspects of the thermophysiology of the skink *Leiolopisma zelandica*. Unpublished PhD thesis, University of Canterbury, Christchurch

Newman DG (1982) New Zealand herpetology. New Zealand Wildlife Service Occasional Publication No. 2, Department of Internal Affairs, Wellington.

Nielsen SV, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol 59:1–22

Olsson M, Shine R (1999) Plasticity of reproduction in an alpine lizard, *Niveoscincus microlepidotus*. Copeia 1999:794–796

Parrish GR, Gill BJ (2003) Natural history of the lizards of the Three Kings Islands, New Zealand. N Z J Zool 30:205–220

Patterson GB, Daugherty CH (1990) Four new species and one new subspecies of skinks, genus *Leiolopisma* (Reptilia: Lacertilia: Scincidae) from New Zealand. J R Soc N Z 20:65–84

Penniket S (2012) Trends in body size and female reproductive frequency with elevation and temperature in a primarily nocturnal, viviparous gecko. Unpublished MSc thesis, University of Otago, Dunedin

Penniket S, Cree A (2015) Adherence to Bergmann's rule by lizards may depend on thermoregulatory mode: support from a nocturnal gecko. Oecologia 178:427–440

Porter R (1987) An ecological comparison of two *Cyclodina* skinks (Reptilia: Lacertilia) in Auckland, New Zealand. N Z J Zool 14:493–507

Porter WP (1967) Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. Ecol Monogr 37:273–296

Rivera S (2008) Health assessment of the reptilian reproductive tract. J Exot Pet Med 17:259–266

Robinson M (1985) Sexual cycles of New Zealand lizards, with particular reference to the gecko *Hoplodactylus maculatus* (Boulenger). MSc thesis, Victoria University of Wellington, Wellington

Rock J (1999) The relationship between thermal biology and female reproduction in the viviparous gecko, *Hoplodactylus maculatus*. Unpublished PhD thesis, University of Otago, Dunedin

Rock J (2006) Delayed parturition: constraint or coping mechanism in a viviparous gekkonid? J Zool 268:355–360

Rock J, Cree A (2003) Intraspecific variation in the effect of temperature on pregnancy in the viviparous gecko *Hoplodactylus maculatus*. Herpetologica 59:8–22

Rock J, Andrews RM, Cree A (2000) Effects of reproductive condition, season and site on selected temperatures of a viviparous gecko. Physiol Biochem Zool 73:344–355

Rock J, Cree A (2008) Extreme variation in body temperature in a nocturnal thigmothermic lizard. Herpetol J 18:69–76

Romijn RL (2013) Can skinks recover in the presence of mice? Unpublished BSc(Hons) dissertation, Victoria University of Wellington, Wellington

Rowlands RPV (1999) New Zealand geckos. A guide to captive maintenance and breeding. Revised edn. EcoPrint, Auckland

Rowlands R (2000) Natural history, care and breeding of Duvaucel's gecko *Hoplodactylus duvaucelii*. Gekko 1:22–27

Saint Girons H, Newman DG (1987) The reproductive cycle of the male tuatara, *Sphenodon punctatus,* on Stephens Island, New Zealand. N Z J Zool 14:231–237

Scharf I, Meiri S (2013) Sexual dimorphism of heads and abdomens: different approaches to 'being large' in female and male lizards. Biol J Linn Soc 110:665–673

Scharf I, Feldman A, Novosolov M, Pincheira-Donoso D, Das I, Böhm M, Uetz P, Torres-Carvajal O, Bauer A, Roll U, Meiri S (2015) Late bloomers and baby boomers: ecological drivers of longevity in squamates and the tuatara. Glob Ecol Biogeogr 24:396–405

Sheehan H (2002) Age at maturity, longevity and sexual size dimorphism in a sub-alpine population of common geckos (*Hoplodactylus maculatus*): a comparison with warmer populations. Unpublished BSc(Hons) dissertation, University of Otago, Dunedin

Sheehan H, Rock J, Girling J, Cree A (2004) Remarkable delay in maturity and great longevity in a sub-alpine population of common geckos (*Hoplodactylus maculatus*). Proceedings of the 10th Biennial conference of the Society for Research on Amphibians and Reptiles in New Zealand. N Z J Zool 31:109

Shine R (2014) Evolution of an evolutionary hypothesis: a history of changing ideas about the adaptive significance of viviparity in reptiles. J Herpetol 48:147–161

Southey IC (1985) The ecology of three rare skinks on Middle Island, Mercury Islands. Unpublished MSc thesis, University of Auckland, Auckland

Spencer NJ, Thomas BW, Mason RF, Dugdale JS (1998) Diet and life history variation in the sympatric lizards *Oligosoma nigriplantare polychroma* and *Oligosoma lineoocellatum*. N Z J Zool 25:457–463

Stewart JR, Blackburn DG (2015) Viviparity and placentation in lizards. In: Rheubert JL, Siegel DS, Trauth SE (eds) Reproductive biology and phylogeny of lizards and tuatara. CRC Press, Taylor and Francis Group, Boca Raton, FL, pp 448–563

Thomas BW (1981) *Hoplodactylus rakiurae* n. sp. (Reptilia: Gekkonidae) from Stewart Island, New Zealand, and comments on the taxonomic status of *Heteropholis nebulosus* McCann. N Z J Zool 8:33–47

Tingley R, Hitchmough RA, Chapple DG (2013) Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol Conserv 165:62–68

Tocher MD (2009) Life history traits contribute to decline of the critically endangered lizards at Macraes Flat, Otago. N Z J Ecol 33:125–137

Todd A (2003) Mating strategies and sperm competition in New Zealand geckos (Family Gekkonidae). Unpublished PhD thesis, University of Canterbury, Christchurch

Todd AC (2005) The social mating system of *Hoplodactylus maculatus*. N Z J Zool 32:251–262

Todd A (2008) Using testis size to predict the mating systems of New Zealand geckos. N Z J Zool 35:103–114

Tokarz RR, Summers CH (2011) Stress and reproduction in reptiles. In: Norris DO, Lopez KH (eds) Hormones and reproduction of vertebrates, vol 3, Reptiles. Academic, London, pp 169–213

Towns DR (1975) Reproduction and growth of the black shore skink, *Leiolopisma suteri* (Lacertilia: Scincidae), in north-eastern New Zealand. N Z J Zool 2:409–423

Towns DR (1994) The role of ecological restoration in the conservation of Whitaker's skink (*Cyclodina whitakeri*), a rare New Zealand lizard (Lacertilia: Scincidae). N Z J Zool 21:457–471

Towns DR, Ferreira SM (2001) Conservation of New Zealand lizards (Lacertilia: Scincidae) by translocation of small populations. Biol Conserv 98:211–222

Towns DR, Hitchmough RA, Perrott J (2016) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? In: Chapple DG (ed) New Zealand lizards. Springer, Cham, pp 293–320

Vitt LJ (2015) Lizard reproduction: a history of discovery. In: Rheubert JL, Siegel DS, Trauth SE (eds) Reproductive biology and phylogeny of lizards and tuatara. CRC Press, Taylor and Francis Group, Boca Raton, FL, pp 1–26 + plate p 699

While GM, Halliwell B, Uller T (2015) The evolutionary ecology of parental care in lizards. In: Rheubert JL, Siegel DS, Trauth SE (eds) Reproductive biology and phylogeny of lizards and tuatara. CRC Press, Taylor and Francis Group, Boca Raton, FL, pp 590–619

Whitaker AH (1968) *Leiolopisma suteri* (Boulenger), an oviparous skink in New Zealand. N Z J Sci 11:425–432

Whitaker AH (1982) Interim results from a study of *Hoplodactylus maculatus* (Boulenger) at Turakirae Head, Wellington. In: Newman DG (ed) New Zealand Herpetology. New Zealand Wildlife Service Occasional Publication No. 2. Department of Internal Affairs, Wellington, pp 363–374

Whitaker AH (1994) Research on the harlequin gecko (*Hoplodactylus rakiurae*) at Port Pegasus, Stewart Island, 30 Nov–5 Dec 1992. Society for Research on Amphibians and Reptiles in New Zealand, Motueka

Wilson J (2010) Population viability and resource competition on North Brother Island: conservation implications for tuatara (*Sphenodon punctatus*) and Duvaucel's geckos (*Hoplodactylus duvaucelii*). Unpublished MSc thesis, Victoria University of Wellington, Wellington

Wilson JL (1998) The relationship between body temperature and gestation length in Otago lizard species. Unpublished BSc (Hons) dissertation, University of Otago, Dunedin

Wilson JL, Cree A (2003) Extended gestation with late-autumn births in a cool-climate, viviparous gecko from southern New Zealand (Reptilia: *Naultinus gemmeus*). Austral Ecol 28:339–348

Chapter 8
Diseases of New Zealand Reptiles

Brett Gartrell

> *“And so, as this diseased lizard became offensive, yet still living (though not eating), dirtying the others with its discharges, anal now as well as aural, I threw it out into the field” Colenso (1879)*

Abstract There are considerable gaps in our knowledge of the endemic diseases that are present in New Zealand lizards. The area which has received the most attention is the parasites of lizards, but even here the focus of scientific endeavour has, until recently, been on taxonomy of parasites rather than on any pathogenic effects on the host. There are gaps in our knowledge of the effects of reptile diseases that are currently exotic to New Zealand but may threaten our native lizard species if they are introduced by smuggling or legal importation. For the first section of this chapter, I report the results of a retrospective review of post-mortem databases held at the Institute of Veterinary, Animal and Biomedical Sciences at Massey University in New Zealand. Using this information, I identify the major causes of mortality identified in the post-mortem examination of reptiles in New Zealand. Bacterial and mycotic infections were the most commonly identified cause of death for native geckos and tuatara (*Sphenodon punctatus*) and for exotic species of reptiles kept in New Zealand. Renal disease was the most common cause of death identified for native skinks. For the second part of this chapter, I briefly review major diseases and disease agents found in reptiles in New Zealand.

Keywords Bacterial infection • Captive reptiles • Gecko • Mycotic infection • New Zealand • Parasite • Skink • Tuatara

---

B. Gartrell (✉)
Wildbase, Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Palmerston North, New Zealand
e-mail: B.Gartrell@massey.ac.nz

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_8

8.1 Causes of Mortality of Reptiles in New Zealand

While this book is focused on the New Zealand lizards, I have chosen to include disease information on tuatara (*Sphenodon punctatus*) and some exotic reptiles found in New Zealand. The rationale for this is that many of the diseases of these animals will cross into the New Zealand lizards, and secondly, more research has been published on the disease ecology of tuatara and their parasites than for wild New Zealand lizards.

The summary results that follow give an indication of the frequency of common types of disease affecting the major groups of reptiles present in New Zealand. However, the reader should keep in mind the biases present in the information presented here. Most of the native reptiles submitted for post-mortem examination in New Zealand are captive animals or are part of conservation programmes involving keeping reptiles in short-term captivity during translocations or for research purposes. The number of wild native reptiles submitted for post-mortem examination is comparatively low. Other limitations of the data set include the number of animals that were submitted for post-mortem examination in an advanced state of decomposition, which is especially true for wild reptiles. Small reptiles begin to decompose and desiccate very quickly after death, which often limits the extent of the diagnostic investigation that can be performed and the confidence with which a diagnosis can be made. As such, the most common category of diagnosis in New Zealand reptiles in the post-mortem databases is “unknown cause of death”. Further defining the limits of confidence around the post-mortem examination findings is the variation in the extent of the post-mortem diagnostic investigation carried out; current funding allows for only gross and histological examination of post-mortem specimens. Some limited bacterial cultures and parasitological analyses are also routinely carried out. However, the constraints in funding mean that further testing for many diseases such as toxicology, specific molecular diagnostics and virology cultures is not routinely performed. As a result, the summary diagnoses reported here are very likely to under-represent the incidence of certain types of disease, including toxicoses, viral diseases, rickettsial disease such as chlamydiosis, haemoparasites and systemic protozoal disease. The final caveat is that many parasites found at post-mortem examination are often not identified beyond a broad classification of type.

8.1.1 Causes of Mortality in Native Reptiles in New Zealand

The retrospective analysis of wildlife post-mortem databases identified a total of 335 post-mortem investigations on native New Zealand reptiles over the period of 1991–2015. These investigations included 89 tuatara, 115 skinks from 15 species, 120 geckos from 13 species, 2 yellow-bellied sea snakes (*Pelamis platurus*) and 9 sea turtles (green *Chelonia mydas*, $n = 5$; olive ridley *Lepidochelys olivacea*,

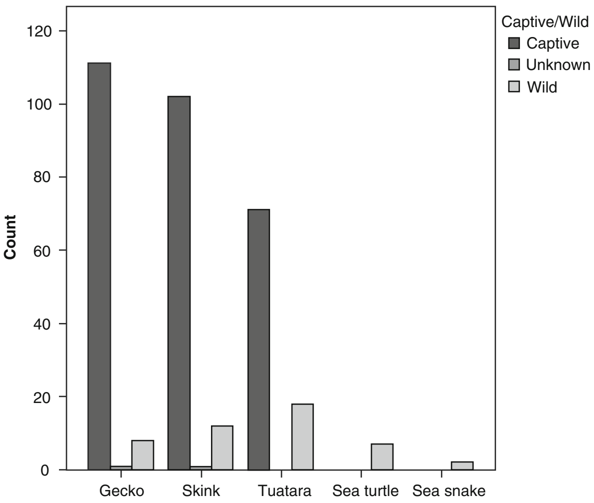


Fig. 8.1 Origin (captive vs wild) of New Zealand reptiles submitted for post-mortem investigation over the period of 1991–2015

$n = 2$; hawksbill *Eretmochelys imbricata*, $n = 1$; leatherback *Dermochelys coriacea*, $n = 1$). Of these animals, 284 were from captivity, 49 were wild animals, and in two cases, the origin of the specimens was not recorded (Fig. 8.1). Given the low numbers of marine reptiles investigated, they will not be further discussed here.

The major causes of mortality are shown in Fig. 8.2. The data under-represents predation as a cause of death for wild New Zealand reptiles, which reflects the biases of the animals' origin and reasons for submission for post-mortem examination. As previously discussed, there are a large number of animals where a diagnosis of the cause of death was unable to be made. Of the investigations where a diagnosis was made, there was a predominance of cases where bacterial or fungal agents were identified as the primary cause of death.

The causes of death for native reptiles were then examined separately for tuatara (Sphenodontidae), skinks (Scincidae, Eugongylinae) and geckos (Diplodactylidae). This revealed different patterns of mortality between the groups (Fig. 8.3a, b, c). While infectious disease due to bacterial and fungal (mycotic) agents was common in all groups, geckos and tuatara were more likely to die of bacterial or fungal infections, while the leading identified cause of mortality in skinks was renal (kidney) failure. Fighting among conspecifics (intraspecific trauma) was also more common in skinks and tuatara than geckos. In tuatara, common causes of mortality included feeding accidents, resulting in intestinal complications such as obstructions, intussusceptions and perforations. Nutritional disease in tuatara was mostly related to metabolic bone disease associated with dietary imbalances and a lack of exposure to adequate amounts of ultraviolet-B (UV-B) light.

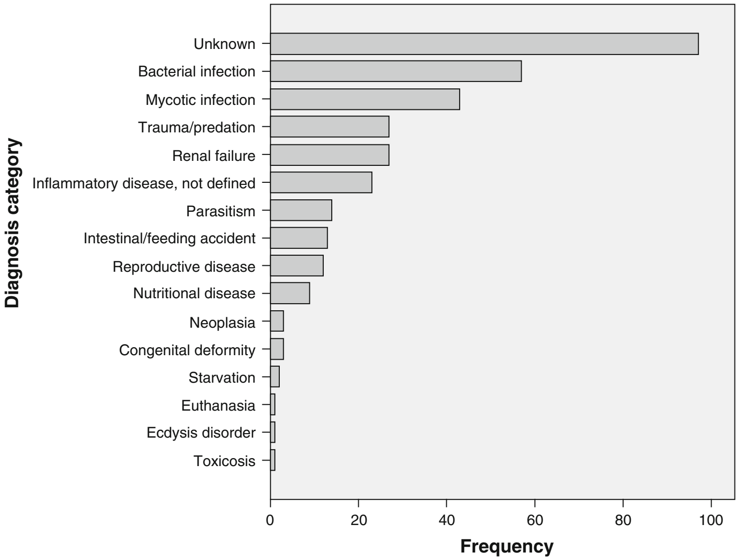


Fig. 8.2 Categories of causes in death identified at post-mortem investigation of New Zealand native reptiles over the period 1991–2015

8.1.2 Causes of Mortality in Exotic Reptiles in New Zealand

The frequency of causes of mortality identified in exotic reptile species in New Zealand was similar to that of native reptiles, with bacterial and fungal infections predominating (Fig. 8.4). However, diseases associated with problems in husbandry, such as renal failure, intestinal accidents and nutritional disease, were very common, and trauma and predation as a cause of death were comparatively rare. Interestingly, neoplastic disease was more common in these exotic pet reptiles than in native New Zealand reptiles.

8.2 Specific Diseases and Disease Agents of New Zealand Reptiles

8.2.1 Bacterial Disease

8.2.1.1 Salmonellosis

Salmonella spp. comprise an important genus of bacteria that are common in reptiles worldwide. Infections with *Salmonella* spp. are capable of causing severe disease in mammals (including humans) and birds but are usually carried by reptiles as intestinal colonisers with little demonstrable effect on the host. However,

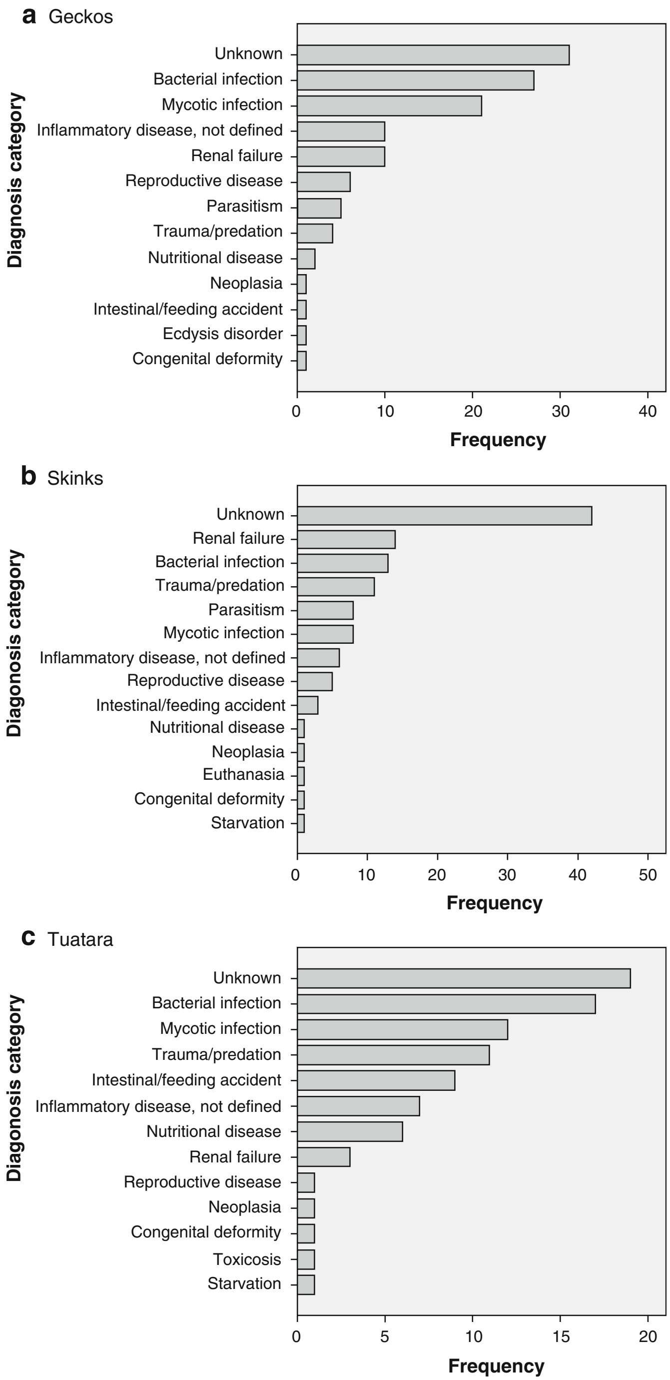


Fig. 8.3 Categories of causes of death identified at post-mortem investigations of (A) New Zealand native geckos, (B) New Zealand native skinks and (C) tuatara, between 1991 and 2015

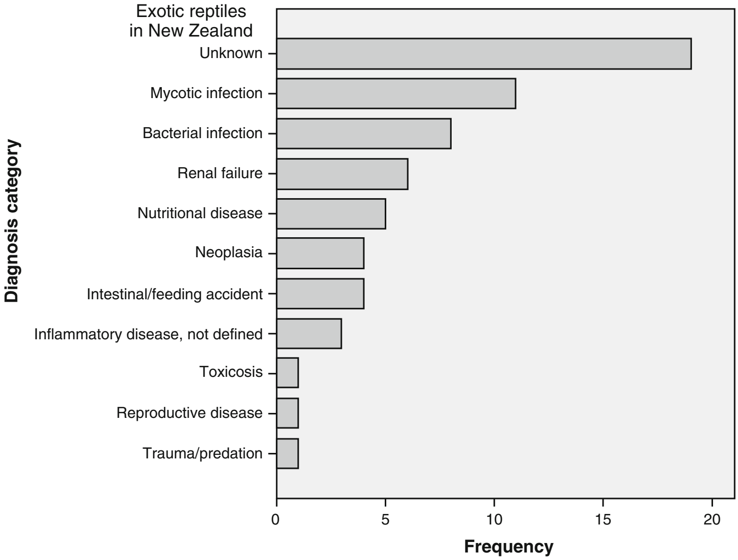


Fig. 8.4 Categories of causes of death identified at post-mortem investigation of exotic species of reptiles kept in captivity in New Zealand over the period of 1991–2015

Salmonella spp. can be occasional causes of disease and death in reptiles. In particular, they are often associated with reproductive disorders, such as ovarian stasis and metritis in reptiles (Le Souëf et al. 2015).

The prevalence of *Salmonella* spp. in native New Zealand reptiles has been studied both in wild populations and in some captive colonies. In native skinks and geckos, a wide variety of *Salmonella* serovars (strains) are present in New Zealand. Middleton et al. (2010) isolated 11 serovars of *S. enterica*, including *S.* Bousso, *S.* Warragul, *S.* Mississippi, *S.* Mana and *S.* Saintpaul with a mean prevalence of 4.7 %. The serovars of *Salmonella* spp. present in native skinks and geckos varied geographically on offshore islands, and this is an important consideration when planning translocations (Baling et al. 2013; Middleton et al. 2010). Current translocation practice in New Zealand and release of captive-bred reptiles regularly ignore the implications of mixing this geographical diversity of strains on the microbial ecology and evolution of *Salmonella* species.

In captive exotic reptiles in New Zealand, the prevalence of *Salmonella* infection was higher (11.4 %) than in wild native lizards, and the diversity of serovars isolated different (Kikillus et al. 2011). The only serovar in common to both native and exotic reptiles in New Zealand was *S.* Infantis. Many of the serovars of *Salmonella* spp. isolated from New Zealand reptiles have known pathogenicity in humans, including *S.* Infantis, which is one of the most common serovars isolated from humans in New Zealand (Broughton et al. 2010).

Unlike other reptiles, tuatara appear to be resistant to colonisation or infection with *Salmonella*. In over 1000 captive and wild tuatara sampled to date (Gartrell et al. 2006, 2007; Middleton et al. 2014), there is only a single case of *Salmonella* (*S. enterica* var houtenae) being detected at post-mortem examination, from the liver of a dead tuatara (van Andel et al. 2015). This lack of colonisation or infection does not reflect lack of exposure as tuatara on Stephens Island/Takapourewa were living in burrows in which *Salmonella* spp. were isolated from soil and cohabiting skinks (Middleton et al. 2014). Investigation of tuatara immunity has established that tuatara serum has strong antibacterial agents effective against *Salmonella* spp. in vitro and also that tuatara mount a robust antibody response associated with environmental exposure to *Salmonella* spp. (Middleton et al. 2015).

In summary, salmonellosis is an important disease of New Zealand reptiles, more known for its potential for zoonotic infection to people handling reptiles than to reptiles themselves but also as an occasional cause of disease and death in reptiles.

8.2.1.2 Other Bacterial Agents

A wide range of other bacterial agents have been shown to cause disease in New Zealand reptiles, and these can be associated with a variety of disease presentations including, but not limited to, osteomyelitis, dermatitis, septicaemia, hepatitis, nephritis and reproductive tract infections. Most of the agents isolated at post-mortem examination of New Zealand reptiles are not primary pathogens, but instead are opportunistic pathogens able to take advantage of breaches in the reptiles' immune defences as a result of inappropriate husbandry, diet or concomitant stress and trauma.

The genera of bacterial agents cultured in New Zealand from diseased reptile tissues at post-mortem examinations or biopsies include *Acinetobacter*, *Actinobacillus*, *Bacillus*, *Citrobacter*, *Corynebacterium*, *Enterobacter*, *Escherichia coli*, *Hafnia*, *Pseudomonas*, *Proteus*, *Salmonella*, *Serratia*, *Staphylococcus*, *Streptococcus* and *Vibrio* spp. The role of these organisms as primary pathogens, opportunistic pathogens, post-mortem invaders or commensal organisms is often unclear.

Recently, a *Rickettsia*-like organism was found in the cytoplasm of the erythrocytes of a Duvaucel's gecko (Barry et al. 2011). The organism was identified by light microscopic examination of blood smears but not further characterised. *Rickettsia* species are obligate intracellular parasites that belong to the Proteobacteria. They are usually spread by invertebrate vectors and can cause significant disease in humans (e.g., spotted fever and murine typhus), although their significance to reptiles is unknown.

8.2.2 Mycotic Diseases

8.2.2.1 *Parranannizziopis australensis*

A newly emerging fungal disease of reptiles caused by *Parranannizziopis australensis* (PA) has been identified in captive tuatara and bearded dragons in New Zealand. This organism was previously known as the *Chrysosporium* anamorph of *Nannizziopsis vriesii* (CANV) and has been responsible for fatal dermatitis in many reptile species throughout the world (Sigler et al. 2013). PA has caused fatal dermatitis in the bearded dragon in New Zealand but has so far only caused a mild dermatitis that responds well to treatment in captive tuatara (Alexander 2014). The presence and prevalence of this organism in wild tuatara populations and other New Zealand native reptiles is currently unknown. In tuatara, the fungus causes ulcers or caseous nodules to develop on the skin of the ventral surfaces.

8.2.2.2 Black Spot Dermatitis

A common condition of native New Zealand geckos is a superficial mycotic dermatitis that usually results in a black powdery growth on the scales (Fig. 8.5) that disappears after successful ecdysis, but can occasionally cause a deeper dermatitis that causes incomplete ecdysis, systemic disease and sometimes death (Gartrell and Hare 2005). The fungi *Cladosporium cladosporioides*, *Alternaria alternata* and *Mucor ramosissimus* have been implicated in this condition. Mycotic dermatitis is common in captive reptiles and generally secondary to problems with husbandry or defective ecdysis (Hellebuyck et al. 2012). In a study of the cutaneous mycobiota of healthy captive reptiles in the United States of America, fungi of 50 genera were isolated from 127 reptiles, which gives an indication of the variety of saprophytic fungi that normally live on the surface of reptile skin (Paré 2013). Most authors believe that mycotic dermatitis is usually caused by these saprophytes invading tissues (Gartrell and Hare 2005; Mader 2006; Paré 2013).

8.2.2.3 Other Mycotic Diseases

Similar to the bacteria described above, a variety of fungi are often cultured from the tissues of reptiles at biopsy and post-mortem examination. It is again often unclear as to whether these fungi are primary pathogens, opportunistic pathogens talking advantage of compromises in the hosts' immune system or, in the case of dead animals, post-mortem invaders from the saprophytic environment. Outbreaks of fungal disease in captive reptiles are often associated with inappropriate temperature and humidity in the captive environment, and proliferation of fungus in the artificial habitat.

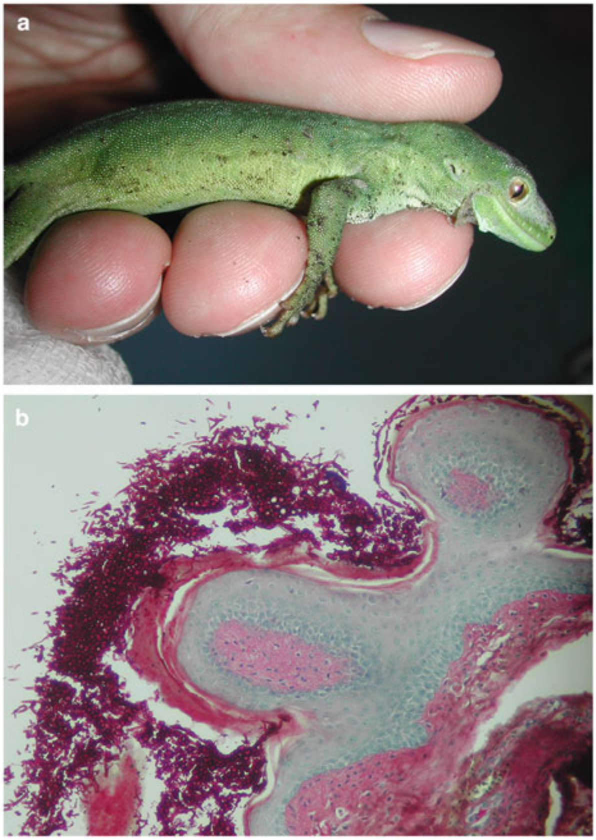


Fig. 8.5 Marlborough green gecko (*Naultinus manukanus*) showing (**a**) the powdery black changes to the skin consistent with black spot mycotic dermatitis. Note the clean skin under the jaw where ecdysis has commenced. (**b**) The histological appearance of a biopsy of the skin from the same gecko showing fungal mats on the skin's surface stained purple with PAS stain

The culture and identification of reptile fungi is problematic, and many post-mortem reports from reptiles in New Zealand show that a fungus has been cultured but not identified to species. The fungal genera cultured from diseased tissues in New Zealand reptiles include *Alternaria*, *Aspergillus*, *Beauveria*, *Candida*, *Cladosporium*, *Mucor*, *Paecilomyces*, *Parranannizziopis*, *Penicillium* and *Rhizopus* spp.

8.2.3 Viral Disease

Only one viral disease of reptiles has been diagnosed in a New Zealand reptile. A bearded dragon seized as a smuggled animal died in quarantine and was diagnosed at post-mortem examination as suffering from an adenovirus infection causing fatal hepatitis (Julian and Durham 1982). As yet, this viral disease has not been seen in the wider captive reptile populations and the effect of adenovirus on native reptiles is unknown.

It should be noted that globally, there is increasing recognition of the importance of viral disease in reptiles. Herpesvirus, paramyxovirus, ranavirus, reovirus and rhabdovirus have all been associated with outbreaks of infectious disease in reptiles outside of New Zealand (Latney and Wellehan 2013). It is possible that viral disease is present in New Zealand reptiles but undiagnosed. However, the geographical isolation of New Zealand and strict limits on legal importation of reptiles may have prevented the establishment of some of these diseases, and their effects on New Zealand native reptiles are largely unknown. The illegal and accidental importation of reptiles into New Zealand is the most likely route of entry for many of these viruses (Maria 2014; Chapple et al. 2016).

8.2.4 Parasitic Disease

The parasites of New Zealand reptiles have been the subject of some study by taxonomists, and the recent use of molecular techniques is revealing that previous studies based on morphological taxonomy have erroneously classified some parasites and underestimated the diversity of other groups (Mockett 2015). It is very likely that emerging molecular techniques will reveal a much greater diversity of parasites than is currently known (Poulin 2014). Rather than provide a detailed timeline of parasite taxonomic research in New Zealand reptiles, I have chosen to provide as a table a checklist of recorded host-parasite associations (Table 8.1), modified from a previous review (McKenna 2003) and updated by changes in host taxonomy (Hitchmough et al. 2016) and recent relevant publications (Barry et al. 2011; Gartrell and Hare 2005; Godfrey et al. 2008, 2010a, 2011a, b; Herbert et al. 2010; Reardon and Norbury 2004; Mockett 2015). I then focus on the broad groups of parasites that have been found in reptiles in New Zealand and review the studies that explore the effects of these parasites on their reptile hosts. With the notable exception of studies of tuatara (Godfrey et al. 2008, 2010a, 2011a, b; Herbert et al. 2010), disease ecology studies on host-parasite interactions in New Zealand reptiles are largely lacking.

One of the challenges for conservationists is how to retain native parasite assemblages while minimising their pathogenic effects on their hosts (Gómez and Nichols 2013). This can become especially problematic in captive reptiles or when translocating reptiles as either parasite numbers or their effects can be amplified by captive conditions. The stress of capture, translocation and the re-establishment of new territories may also diminish the host's immune response, which ordinarily keeps parasites in check. If animals are healthy and the parasites are already present at the translocation site, then it is recommended to move the parasites with the host or attempt to reduce their numbers without eliminating them completely (Stringer and Linklater 2014). However, in captivity, control of parasites is usually necessary to prevent disease and mortality.

Table 8.1 Host-parasite associations recorded in native New Zealand reptiles

Host species	Previous host name (if applicable)	Parasite phylum	Parasite species
Native New Zealand reptiles			
Pacific gecko (*Dactylocnemis pacificus*)	*Hoplodactylus pacificus*	Acari	*Geckobia hoplodactyli*
			Ophionyssus sp.
		Nematoda	*Skrjabinodon poicilandri*
			Skrjabinodon sp.
		Trematoda	*Paradistomum pacificus*
		Protozoa	*Hepatozoon lygosomarum*[a]
Duvaucel's gecko (*Hoplodactylus duvaucelii*)		Acari	*Amblyomma sphenodonti*
			Geckobia hoplodactyli
			Geckobia naultina
			Neotrombicula naultini
			Ophionyssus galeotes
			Ophionyssus sp.
		Nematoda	*Skrjabinodon poicilandri*
			Skrjabinodon sp.
		Protozoa	*Hepatozoon lygosomarum*[a]
Forest gecko (*Mokopirirakau granulatus*)	*Hoplodactylus granulatus*	Nematoda	*Skrjabinodon poicilandri*
Auckland green gecko (*Naultinus elegans*)	*Naultinus elegans elegans*	Acari	*Geckobia naultina*
Jewelled gecko (*Naultinus gemmeus*)		Acari	*Neotrombicula naultini*
Northland green gecko (*Naultinus grayii*)		Nematoda	*Skrjabinodon poicilandri*
Marlborough green gecko (*Naultinus manukanus*)		Protozoa	*Nyctotherus* sp.
			Trichomonas sp.
Nelson green gecko (*Naultinus stellatus*)		Nematoda	*Skrjabinodon poicilandri*
Wellington green gecko (*Naultinus punctatus*)	*Naultinus elegans punctatus*	Acari	*Geckobia naultina*
Copper skink (*Oligosoma aeneum*)	*Cyclodina aenea*	Nematoda	*Parathelandros* sp.
			Skrjabinodon trimorphi[b]
		Cestoda	*Baerietta decidua*
Robust skink (*Oligosoma alani*)	*Cyclodina alani*	Acari	*Amblyomma sphenodonti*
Green skink (*Oligosoma chloronoton*)		Nematoda	*Skrjabinodon trimorphi*

(continued)

Table 8.1 (continued)

Host species	Previous host name (if applicable)	Parasite phylum	Parasite species
Grand skink (*Oligosoma grande*)		Acari	*Acomatacarus lygosomae*
			Odontacarus lygosomae
			Ophionyssus scincorum
		Nematoda	*Skrjabinodon trimorphi*[b]
		Protozoa	*Hepatozoon lygosomarum*[a]
Chevron skink (*Oligosoma homalonotum*)		Nematoda	*Skrjabinodon* sp.[b]
			Skrjabinodon trimorphi[b]
Cryptic skink complex[c] (*Oligosoma inconspicuum*)	*Oligosoma inconspicuum*	Nematoda	*Skrjabinodon trimorphi*[b]
Speckled skink (*Oligosoma infrapunctatum*)		Acari	*Neotrombicula sphenodonti*
		Nematoda	*Capillaria* sp.
			Hedruris minuta
			Parathelandros sp.
			Skrjabinodon trimorphi[b]
		Trematoda	*Dolichosaccus* (*Lecithopyge*) *leiolopismae*
		Protozoa	*Hepatozoon lygosomarum*[a]
Spotted skink (*Oligosoma lineoocellatum*)		Acari	*Acomatacarus lygosomae*
			Neotrombicula sphenodonti
			Ophionyssus scincorum
		Nematoda	*Parathelandros* sp.
			Skrjabinodon trimorphi[b]
		Cestoda	*Oochoristica novaezealandicae*
		Trematoda	*Dolichosaccus* (*Lecithopyge*) *leiolopismae*
			Paradistomum pacificus
		Protozoa	*Hepatozoon lygosomarum*[a]
McCann's skink (*Oligosoma maccanni*)		Acari	*Odontacarus lygosomae*
			Ophionyssus scincorum
		Nematoda	*Skrjabinodon trimorphi*[b]
		Protozoa	*Hepatozoon lygosomarum*[a]

(continued)

Table 8.1 (continued)

Host species	Previous host name (if applicable)	Parasite phylum	Parasite species
Small-scaled skink (*Oligosoma microlepis*)		Nematoda	*Skrjabinodon trimorphi*[b]
Moko skink (*Oligosoma moco*)		Acari	*Ophionyssus scincorum*
Marbled skink (*Oligosoma oliveri*)		Acari	*Ophionyssus* sp.
Ornate skink (*Oligosoma ornatum*)	*Cyclodina ornata*	Acari	*Ophionyssus* sp.
Otago skink (*Oligosoma otagense*)		Acari	*Neotrombicula naultini*
			Odontacarus lygosomae
			Ophionyssus scincorum
		Nematoda	*Parathelandros* sp.
			Skrjabinodon trimorphi[b]
		Protozoa	*Hepatozoon lygosomarum*[a]
Common skink (*Oligosoma polychroma*)[d]	*Oligosoma nigriplantare*	Acari	*Acomatacarus lygosomae*
			Neotrombicula naultini
			Neotrombicula sphenodonti
			Odontacarus lygosomae
			Ophionyssus scincorum
		Nematoda	*Hedruris minuta*
			Parathelandros sp.
			Pharyngodon sp.
			Skrjabinodon trimorphi[b]
		Cestoda	*Baerietta allisonae*
			Baerietta decidua
			Oochoristica novaezealandicae
		Trematoda	*Dolichosaccus* (*Lecithopyge*) *leiolopismae*
			Paradistomum pacificus
		Protozoa	*Hepatozoon lygosomarum*[a]
Shore skink (*Oligosoma smithi*)		Nematoda	*Hedruris minuta*
		Protozoa	*Hepatozoon lygosomarum*[a]
Egg-laying skink (*Oligosoma suteri*)		Acari	*Ophionyssus* sp.
		Nematoda	*Skrjabinodon* sp.[b]
			Skrjabinodon trimorphi[b]

(continued)

Table 8.1 (continued)

Host species	Previous host name (if applicable)	Parasite phylum	Parasite species
Brown skink (*Oligosoma zelandicum*)		Acari	*Acomatacarus lygosomae*
			Neotrombicula sphenodonti
		Nematoda	*Parathelandros* sp.
			Skrjabinodon trimorphi[b]
Tuatara (*Sphenodon punctatus*)		Acari	*Amblyomma sphenodonti*[e]
			Neotrombicula naultini
			Neotrombicula sphenodonti
		Nematoda	*Hatterianema hollandei*
		Trematoda	*Dolichosaccus* (*Lecithopyge*) *leiolopismae*
		Protozoa	*Hepatozoon tuatarae*[f]
			Microsporidium sp.
			Trichomonas sp.
Striped gecko (*Toropuku stephensi*)	*Hoplodactylus stephensi*	Nematoda	*Skrjabinodon poicilandri*
Harlequin gecko (*Tukutuku rakiurae*)	*Hoplodactylus rakiurae*	Nematoda	*Skrjabinodon poicilandri*
Common gecko (*Woodworthia maculata*)[g]	*Hoplodactylus maculatus*	Acari	*Geckobia hoplodactyli*
			Microtrombicula hoplodactyla
			Neotrombicula naultini
			Ophionyssus galeotes
		Nematoda	*Parathelandros* sp.
			Skrjabinodon poicilandri
			Skrjabinodon sp.
		Cestoda	*Baerietta allisonae*
		Trematoda	*Paradistomum pacificus*
		Protozoa	*Eimeria* sp.
			Entamoeba sp.
			Hepatozoon lygosomarum[a]
			Nyctotherus sp.
			Trichomonas hoplodactyli
Exotic reptiles in New Zealand (including border interceptions)			
Indian blood sucker lizard (*Calotes versicolor*)		Nematoda	*Pterygosoma* sp.

(continued)

Table 8.1 (continued)

Host species	Previous host name (if applicable)	Parasite phylum	Parasite species
Flat-tailed gecko (*Cosymbotus platyurus*)		Acari	*Geckobia philippinensis*
Oceanic gecko (*Gehyra oceanica*)		Acari	*Geckobia carcinoides*
			Geckobia gehyrae
			Geckobia keegani
Tokay gecko (*Gekko gecko*)		Acari	*Geckobia bataviensis*
Oriental leaf-toed lizard (*Hemidactylus bowringii*)		Acari	*Geckobia gehyrae*
Pacific house gecko (*Hemidactylus frenatus*)		Acari	*Geckobia bataviensis*
			Geckobia indica
			Geckobia keegani
			Geckobia philippinensis
			Pimeliaphilus sp.
Indo-Pacific gecko (*Hemidactylus garnotii*)		Acari	*Geckobia bataviensis*
			Geckobia gehyrae
Tropical house gecko (*Hemidactylus mabouia*)		Acari	*Geckobia tasmani*
Rainbow skink (*Lampropholis delicata*)		Acari	*Geckobia keegani*
Common garden skink (*Lampropholis guichenoti*)		Acari	*Ophionyssus scincorum*
Water dragon (*Physignathus lesueurii*)		Nematoda	*Abbreviata* sp.
Bearded dragon (*Pogona* sp.)		Protozoa	*Isospora amphiboluri*
Bluetongue skink (*Tiliqua scincoides*)		Acari	*Ophionyssus natricis*

Source: Modified from McKenna (2003) with permission and assistance by P. McKenna

[a] Previously *Haemogregarina*

[b] Mockett (2015) proposes reclassifying the *Skrjabinodon* nematode species found in New Zealand skinks to the genus *Spauligodon* while retaining the species reported from New Zealand geckos in *Skrjabinodon*

[c] The cryptic skink complex of *Oligosoma inconspicuum* has been revised (Chapple et al. 2011) to include at least four species: *Oligosoma burganae, Oligosoma repens, Oligosoma toka* and *Oligosoma tekakahu*

[d] The common skink grouping *Oligosoma polychroma* have been revised with *O. polychroma* representing a complex of five species (Liggins et al. 2008; Chapple et al. 2009; Hitchmough et al. 2016). Specimen origin data is not readily available to further define the host-parasite associations within this grouping, so the associations reported here may be unreliable

[e] Previously *Aponomma sphenodonti*

[f] Previously *Haemogregarina tuatara*

[g] The common gecko genus *Woodworthia* includes multiple cryptic lineages (Nielsen et al. 2011; Hitchmough et al. 2016). Specimen origin data are not readily available to further define the host-parasite associations within this genus

8.2.4.1 Ectoparasites

The main types of ectoparasites found on terrestrial New Zealand reptiles are ticks and mites. These parasites do not spend all their lives on the host and so environmental conditions can influence infection rates and disease effects on reptiles (Godfrey et al. 2008, 2010a, b, 2011b). Ticks will cause localised skin damage and may allow entry of secondary pathogens to tissue beneath the skin barriers. In studies outside of New Zealand, ticks have been found to transmit a variety of pathogens to reptiles, including viruses, bacteria (including *Rickettsia*) and haemoparasites. In high numbers, ticks may cause severe anaemia and be fatal. Reptile ticks can also transmit zoonotic pathogens (organisms which cause disease in humans).

Mites are very common in most species of reptiles and often congregate in the axillae, around joints, cloaca, nostrils and eyelids. They may also cause focal skin irritation and have been associated with the transmission of pathogens. In large numbers, they can cause anaemia in the host. The native mite, *Geckobia naultina,* is suspected of being the vector of a *Rickettsia*-like organism in a Duvaucel's gecko (Barry et al. 2011). Reptile mites can also transmit zoonotic disease to humans, although this has not been recorded in New Zealand.

Heath and Whitaker (2015) reported that exotic reptiles intercepted as they arrived in New Zealand carried 4 genera and 16 species of mites. The majority of mites collected were Pterygosomatidae, with just four individuals of one species of Macronyssidae collected. There were 252 batches of lizards infested with *Geckobia bataviensis*, each batch representing a single interception (case) record, irrespective of the number of lizards present. The introduction of exotic reptiles into New Zealand can potentially threaten New Zealand's biosecurity, with both the host and its parasites being vectors of diseases that are of significance to both human and native reptile health.

Ticks can be treated by physical removal, ensuring the head parts are not left embedded. However, for most tick and mite infestations, the oral or topical application of insecticides such as permethrin or ivermectin is used (Mader 2006). The treatment of reptiles with insecticides to control ectoparasites must be undertaken with caution as toxicity is common. The most frequently recommended treatments include oral dosing with ivermectin, or the topical applications of permethrins. Control of acarid stages in the environment is essential in a captive setting. All cage furnishings and substrates should be replaced and the enclosure and reptiles treated simultaneously with permethrins. Using paper as a substrate during treatment times can aid this process. Mite numbers can be reduced, though not eliminated by bathing the reptile in lukewarm water for 30 min. However, this does not clear mites or ticks from the head of the reptile, or the rest of the environment. A light covering of cooking oil has also been used to drown mites on reptiles, but again, this does not control any ectoparasite stages in the environment, so will not eradicate the mites (Mader 2006).

Myiasis (flystrike) has been recorded in *Naultinus* spp. geckos kept in captivity as early as 1880 (Colenso 1879). Flies lays eggs which hatch into larvae (maggots) in open wounds and in the mouth and vent of dead and dying animals. Primary flystrike in reptiles is rarely reported in New Zealand, and most of the *Calliphora* spp. of flies are opportunist wound invaders only and can be safely fed live to healthy reptiles.

However, the following species are able to initiate primary flystrike in most animals (Heath and Bishop 2006) and should not be fed live to captive reptiles; the common green blowfly (*Lucilia sericata*), Australian green blowfly (*Lucilia cuprina*) and the brown blowfly (*Calliphora stygia*).

Treatment of reptiles affected by myiasis involves extracting the maggots individually and/or by lavage with copious amounts of physiological saline and applying a topical disinfectant to the wound (Mitchell and Diaz-Figueroa 2004). Avoid the use of topical insecticides as these can be toxic to the host as discussed above.

8.2.4.2 Endoparasites

Endoparasites of reptiles include the phyla Nematoda (roundworms), Cestoda (tapeworms), Trematoda (flukes) and Protozoa. Nematodes and cestodes are generally confined to the gastrointestinal tract. The appearance of multiple forms of parasite ova in faecal exams of reptiles often suggests a diversity of these parasites that is not reflected in the published host-parasite records (Gartrell et al. 2006). The taxonomy of many of these parasites has been historically based on morphology alone, and recent investigations using DNA sequencing have challenged previous assumptions and classifications. For example, Mockett (2015) examined the nematode parasites of New Zealand skinks and geckos. Her results support reclassifying *Skrjabinodon* nematode species found in New Zealand skinks to *Spauligodon* but retaining *Skrjabinodon* for the species found in New Zealand geckos.

Treatment of heavy nematode burdens in reptiles involves the use of anthelmintics designed for domestic animals species and is considered “off-label” use. Ivermectin, moxidectin and fenbendazole have been used to treat nematodes successfully in New Zealand reptiles, but treatment failure due to inadequate dosing or anthelmintic resistance in the parasites occurs. Toxic effects on the host from overdosing are also common, so careful dosing based on individual weight is very important. Cestodes are best treated with praziquantel.

Trematodes are rare in comparison to nematodes and cestodes, but they do occur in terrestrial reptiles in New Zealand. Trematodes are usually more common in aquatic reptiles, and spirorchid flukes are a major cause of mortality of sea turtles found in Australian waters (Raidal et al. 1998), although they have not yet been reported in turtles stranded in New Zealand.

A range of protozoal species are found regularly in reptile gastrointestinal tracts. These include ciliated protozoa, such as *Balantidium* spp. and *Nyctotherus* spp., and flagellated protozoa, such as *Trichomonas* spp. and *Giardia* spp., as well as the more pathogenic coccidia. The ciliated and flagellated protozoa are usually considered to be commensal organisms that have minimal effects on the host (Mader 2006). In reptiles in poor body condition, high burdens of these protozoa may require treatment with imidazole drugs such as metronidazole, but usually they are best left undisturbed. The coccidial organisms are more likely to be associated with enteritis, diarrhoea and weight loss, and moderate to heavy burdens of these should be treated (Mader 2006). The drugs used for this include trimethoprim/sulfonamide combinations or toltrazuril.

8.2.4.3 Haemoparasites

Haemoparasites (parasites of the blood) have been found in many reptile species in New Zealand, and three species of haemoparasitic protozoa have been described. In general, haemoparasites of reptiles have low level effects on the host, but the research on this is lacking when compared to studies of mammalian and avian haemoparasites.

Hepatozoon tuatarae (previously *Haemogregarina tuatarae*) infects approximately 20 % of the tuatara on Stephens Island at a low level of parasitaemia (Godfrey et al. 2011a, b). A confirmed vector of the organism in tuatara is the tick *Amblyomma sphenodonti* (Herbert et al. 2010). The parasite infects both leucocytes (white cells) and erythrocytes (red cells) within the blood of the host and infected individuals were smaller on average than uninfected hosts (Godfrey et al. 2011a, b).

Hepatozoon lygosomarum (previously *Haemogregarina lygosomarum*) has been found in native New Zealand skink species. A likely vector for this parasite has been identified as the native mite *Ophionyssus scincorum*, whose infection intensity has been associated with the presence of the haemoparasite (Reardon and Norbury 2004), although isolation of the organism from the mites is yet to be confirmed. This study also found a weaker but significant association between infection with *He. lygosomarum* and another mite *Odontocarus lygosomae*. There are no studies of the effect of infection with this parasite on the reptile's health.

A single report identified *Plasmodium lygosomae* in the erythrocytes of two of nine skinks from the Wellington region, identified at the time as Moko skinks, *Lygosoma moco*, by Laird in 1948, but which are subsequently thought to have been common skinks *Oligosoma polychroma* (cited in McKenna 2003; Barry et al. 2011).

In reptiles in other countries, *Hepatozoon* spp. and *Plasmodium* spp. are usually associated with mild anaemia if any disease is seen at all. The parasites' effects may be opportunistically amplified by concurrent disease, or by severe stress that affects the immune system of the host (Mader 2006).

8.2.5 Diseases of Husbandry

There are many diseases associated with keeping reptiles in captivity. It is not the intention of this chapter to fully review these diseases, and readers who require additional information are directed to more detailed texts that focus on reptile disease (e.g. Mader 2006; Mader and Divers 2013). A brief summary of some common diseases associated with husbandry in reptiles in New Zealand is provided below.

8.2.5.1 Renal Disease/Gout

Renal disease (kidney failure) in reptiles is often associated with the deposition of uric acid crystals in body tissues, termed visceral gout (Mader 2006). Renal disease and/or visceral gout was the most common cause of death identified in New Zealand skinks in the retrospective review of post-mortem databases. Gout occurs when the plasma concentrations of uric acid exceed the solubility threshold, leading to precipitation of the crystalline form of uric acid and an accompanying severe inflammatory response. Failure of the kidneys to clear uric acid from circulation due to infection, inflammation or lowered blood flow, as occurs in severe dehydration, is one cause of gout. Another postulated but less likely factor in insectivorous and carnivorous reptiles is that high-protein diets may contribute to this condition since uric acid is the primary end product of protein metabolism in reptiles (Mader 2006). There is no effective treatment for visceral gout once uric acid has crystallised into tissue. The diagnosis of renal disease in live reptiles is made primarily by assessing blood biochemical markers, such as plasma concentrations of uric acid, but this has limitations. Renal disease is treated by addressing the primary cause of the renal disease (if known) and by providing diuretic fluid therapy to maintain renal perfusion and remove collections of uric acid colloids from the ureters. Low-protein, high-carbohydrate diets can be used in the short term to lower the load of uric acid that must be eliminated from the kidneys (Mader 2006).

8.2.5.2 Metabolic Bone Disease

The most common nutritional disorders observed in captive reptiles in New Zealand are metabolic bone disease. This results in deformities and skeletal fractures of young growing reptiles due to diets that have a poor calcium-phosphorus ratio and/or a lack of exposure to sufficient UV-B radiation, which enables the synthesis of vitamin D3 (Burgess et al. 2009). Vitamin D3 is essential for calcium metabolism in all animals, and a diet lacking in it leads to fibrous osteodystrophy in reptiles. This leads to poor bone mineral density, pathological fractures and remodelling of long bones and vertebrae and shortening of the skull

Fig. 8.6 A juvenile tuatara with hypocalcaemia resulting in severe muscle weakness and an inability to stand

(Mader 2006; Mader and Divers 2013). In severe cases, these deficiencies may also cause hypocalcaemia, low blood calcium, that results in muscular weakness, collapse and eventually death (Fig. 8.6).

The diagnosis of metabolic bone disease is usually made by radiography, which shows poor bone density, malformation and fracture of long bones, shortening of the skull and sometimes kyphosis or other malformations of the spine. Bone density can be quantitatively assessed using bone densitometry. Plasma biochemical analysis shows alteration of the calcium-phosphorus ratios in severe cases, but this may not be present in early cases as the homeostatic mechanisms will sacrifice total body calcium reserves to maintain plasma calcium concentrations, due to its importance in cardiac and skeletal muscle functioning (Mader 2006).

If the degree of skeletal deformity is not too advanced, treatment of animals with metabolic bone disease involves fracture stabilisation, analgesia and correction of the diet. Treatment of hypocalcaemic reptiles involves correcting the immediate problem with parenteral or enteral calcium supplementation and then addressing the underlying causes of illness.

Vitamin D metabolism is intimately associated with calcium homeostasis and bone health. Reptiles produce large amounts of vitamin D3 in the skin when exposed to UV-B radiation, and individuals kept outdoors can usually find enough direct sunlight to satisfy this requirement. The importance of exposure to UV-B radiation is evidenced by the possibility that reptiles modify their basking behaviour in response to changing UV light conditions and by a mechanism in the parietal eye of iguanas that can detect UV radiation (Wada et al. 2012).

However, reptiles kept indoors or behind glass, where UV radiation is blocked, are often deficient in vitamin D3 and show an increased incidence of metabolic bone disease (Burgess et al. 2009). The provision of UV-B radiation in the form of fluorescent lights is preferred over dietary supplementation of vitamin D, as vitamin D toxicity can occur. Portable UV-B metres are widely available and should be used to monitor the amount of UV-B reaching basking sites, as the amount of UV-B radiation emitted by these lights varies between and within commercial brands and decreases as the tubes age. Since UV-B output from fluorescent lights diminishes rapidly with distance, these lights should be placed close (20–30 cm in most instances) to substrate level, with nothing between the light and the basking surface. An average intensity of 56 $\mu W/cm^2$ has been measured for UV-B light substrate-level outdoors on a cloudy day in New Zealand, and in the absence of known requirements for New Zealand reptiles, this has been the recommended as the intensity of substrate-level UV-B that should be provided for indoor enclosures (Burgess et al. 2009). This recommended level of UV-B is precautionary, as high levels of UV-B may cause cataract formation in mammals (Cui et al. 2009), although this has yet to be documented in reptiles.

A survey of captive tuatara kept throughout New Zealand showed that a significant proportion were not provided with sufficient access to UV-B light for the synthesis of vitamin D, which may exacerbate the problems created by poor diet. Furthermore, there was a clear relationship between light availability and the historical risk of metabolic bone disease for animals kept indoors (Burgess et al. 2009). Likewise, the roofing material of many outdoor enclosures blocked UV light from reaching basking areas. It is recommended to use wire mesh as the roofs of outdoor enclosures and avoid excessive amounts of shade so that sufficient levels of UV-B reach the ground (Burgess et al. 2009). Tuatara favour basking in the morning, and entrances to burrows should be oriented to allow this (Blanchard 2002).

8.2.5.3 Obesity and Hepatic Lipidosis

Overfeeding of captive animals and limited opportunities or incentives to exercise often lead to a pathological increase in body fat stores. This can interfere with reproductive activity and in severe cases lead to hepatic lipidosis, also known as fatty liver syndrome. In an individual suffering from hepatic lipidosis, the liver is friable and can tear, resulting in fatal intra-coelomic haemorrhage. Counter-intuitively, the condition can also result in anorexia in reptiles (Mader 2006).

Prevention of this condition involves regular weighing and body condition scoring of reptiles to determine appropriate feeding amounts and frequency (Simpson 2006). Consideration should be given to exercise, food items and feeding frequency. One other common aspect to this condition is the apparent prevalence in nonbreeding adult females and aged females. Many female reptiles undergo seasonal cycles of lipogenesis in preparation for folliculogenesis. Those females that do not have the opportunity to breed and produce eggs/young appear more prone to obesity in captivity (Divers and Cooper 2000).

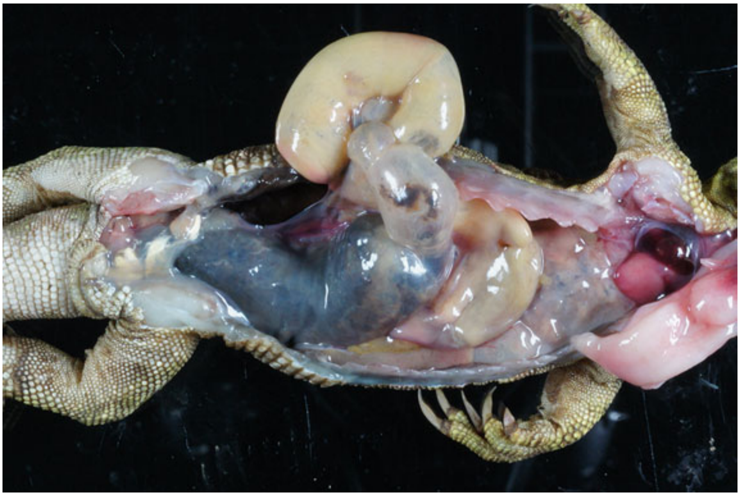


Fig. 8.7 Colonic impaction and intestinal obstruction in a tuatara at post-mortem examination. Photo courtesy of Stuart Hunter, Massey University

8.2.5.4 Feeding Accidents and Intestinal Disorders

A range of gastrointestinal accidents, including perforations, intussusceptions and obstructions (Fig. 8.7), occur in reptiles. An intussusception is the telescoping of one segment of intestine inside another. These intestinal accidents can be caused by inappropriate food items, gastrointestinal infections and/or severe parasitism. Dehydration, among other factors, can result in colonic constipation, which leads to inappetence, or, more fatally, obstruction of urine outflow and renal failure. Tuatara appear to be over-represented in cases of intestinal accidents as causes of mortality due to their less-than-discerning eating habits.

8.2.5.5 Toxicoses

Most toxicities diagnosed in New Zealand reptiles are the result of accidental overdose of medications in captive animals. The post-mortem records indicate that there have been multiple deaths in tuatara due to overdosing with subcutaneous injections of the local anaesthetic, lignocaine, which resulted in widespread musculoskeletal paralysis and death. Several tuatara have also died after receiving vitamin D injections that caused systemic mineralisation of body tissues and death.

Four captive grand skinks (*Oligosoma grande*) died after the topical application of fipronil for the treatment of ectoparasites. The dose applied to the skinks was well in excess of reported toxic doses in other reptiles (Youl 2006). There appears to be two types of toxicity seen with fipronil: acute toxicity, where the animals die within the first week after application, and delayed toxicity, where death occurs up to 4 weeks post-application (Peveling and Demba 2003).

Despite documented evidence of wild native New Zealand reptiles consuming rodenticide baits (Wedding et al. 2010; Freeman et al. 1996; Hoare and Hare 2006), there are no confirmed reports of deaths due to consumption of pest control poisons in New Zealand reptiles. This remains an area of concern, however, and further research into the effects of these poisons on native reptiles is warranted.

8.2.5.6 Temperature-Related Disorders

The expression of disease in reptiles is a result of the complex interaction between pathogens, host immunity and environmental factors. The ectothermic nature of reptiles and the associated need to shuttle between temperatures to regulate their physiology often creates opportunities for otherwise benign micro-organisms to cause disease as discussed above. However, if an appropriate temperature range is not provided for captive reptiles or if temperatures fluctuate widely, this can have complicated flow on effects to reptile health, reproduction and immunity or simply cause direct mortality (Warwick 1991). The ideal temperature range for reptiles is highly species specific and is referred to as the preferred optimal temperature zone (POTZ) (Raske et al. 2012). For more information on thermal physiology of New Zealand lizards, see Hare and Cree (2016). New Zealand lizards are prone to disorders of husbandry associated with heat stress, thermal burns and hypothermia, but these will not be dealt with further here. For more information of these specific problems, see Mader (2006).

8.2.6 Miscellaneous Diseases

8.2.6.1 Reproductive Disorders

Reproductive disease is common in both viviparous and oviparous reptiles, in both captive and wild populations. There is a wide diversity in the reproductive strategies used by reptiles (see Cree and Hare 2016 for more information), and one of the major barriers to identifying a reproductive problem is finding good information on the normal reproductive biology of many species. The discussion below considers the most common diseases associated with ovulation and parturition and egg laying. I have not attempted to cover the management of egg incubation or the disorders that can arise from alterations to the incubation environment, but interested readers are directed to the excellent research on tuatara incubation physiology (Keall et al. 2010; Nelson et al. 2004a, 2010; Thompson 1990) or more general references on reptile incubation (Kohler 2005).

Fig. 8.8 Ovarian stasis (*black arrow*) in a green gecko (*Naultinus*; species not identified further). Also note the digital necrosis present (*white arrow*) which may have resulted from thromboembolism associated with the ovarian infection or dysecdysis associated with the declining body condition of the gecko

8.2.6.1.1 Preovulatory Ovarian Stasis and/or Ovarian Infection

Preovulatory stasis occurs when a reptile undergoes vitellogenesis and develops yolky ovarian follicles that fail to ovulate (Figure 8.8). It occurs in both oviparous and viviparous reptiles and may or may not be associated with bacterial infection of the follicles. *Salmonella* spp. are often isolated from these retained ovarian follicles. The clinical signs associated with this condition include interruption of reproduction, anorexia, lethargy and coelomic distension. The causes of this condition have not been confirmed, but environmental disruption and nutritional deficiencies have been suggested (Le Souëf et al. 2015; Mader 2006; Mader and Divers 2013).

The diagnosis of ovarian stasis is based on the palpation of suspicious masses within the abdomen and then characterising their nature by ultrasonography or laparoscopy. The presence of ovarian follicles outside of the breeding season or the failure of ovarian follicles to progress over time is highly suspicious of ovarian stasis.

No treatment that will maintain the breeding ability of the reptile is currently available for this condition. Surgical removal of the ovaries (ovariectomy) will resolve the clinical signs of disease associated with the condition, but it renders the animal unable to reproduce. Nonetheless, this may be used to salvage animals for display or advocacy purposes (Le Souëf et al. 2015).

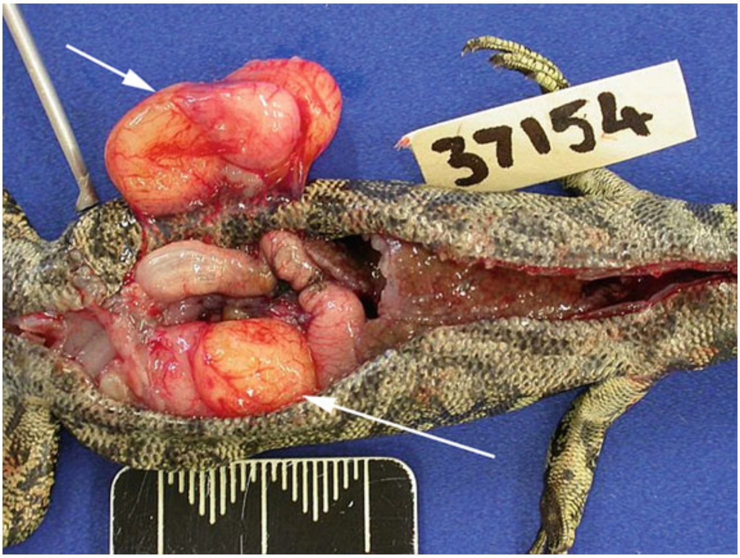


Fig. 8.9 Post-mortem appearance of metritis that resulted in granulomas within the oviduct (*white arrows*) of an Otago skink (*Oligosoma otagense*)

8.2.6.1.2 Metritis

Metritis refers to infections of the oviduct and uterus. This may be due to primary or secondary infections, the presence of retained embryos (see Sect. 8.2.6.1.3 Dystocia) or traumatic damage to the uterus. Inflammatory exudates in reptiles rapidly become caseous, and when infection is present, the oviduct is often filled with granulomatous abscesses. The clinical signs are similar to ovarian stasis and mostly involve cessation of reproductive activity, anorexia and distension of the coelom (Fig. 8.9).

If diagnosed early, treatment of metritis with appropriate antibiotics is theoretically possible, but most cases are diagnosed late in the course of the disease. In valuable breeding animals, treatment may be attempted by surgically opening the oviduct (hysterotomy), removing the infected material and flushing the oviduct, but there is a very high chance that the oviduct will be damaged, resulting in later recurrent infection or dystocia (see 8.2.6.1.3). Surgical removal of the infected oviduct (salpingohysterectomy) is most likely to resolve the clinical signs of disease but will obviously prevent future breeding. The ovaries should also be removed if this is attempted (Mader 2006; Mader and Divers 2013).

8.2.6.1.3 Dystocia

Dystocia refers to difficulties associated with either parturition in viviparous species or oviposition in oviparous reptiles. It appears to be more common in captive reptiles, and abnormal environmental conditions and dietary imbalances or deficiencies are implicated as causal factors in this condition. Dystocia is usually classified as obstructive or functional. Obstructive dystocia is caused by maternal anatomical abnormalities or by physical interference of offspring with the parturition or oviposition. Functional dystocia occurs when there is no obstruction but where the physiological functioning of the oviduct is prevented. This may be due to muscle weakness associated with poor body condition and inactivity or hypocalcaemia resulting from serious nutritional deficiencies. The major difficulty in diagnosing dystocia in reptiles is determining whether the embryo or egg has been retained beyond what is normal for reproduction (Mader 2006; Mader and Divers 2013).

Diagnosis is usually based on a combination of palpation, radiography and/or ultrasonography. Computed tomography and endoscopy may also be used to assess reproductive status of reptiles and are very useful in chelonians.

While treatment of dystocia is not generally an emergency, the longer an egg or embryo is retained, the more chance there is of permanent damage such as scarring and adhesions of the oviduct. In cases of obstructive dystocia, surgical intervention is usually required to resolve the condition. For functional dystocia, the first step is to provide good supportive care for 24–48 h, ensuring a sufficiently humid environment within the POTZ. Oral dosing with a calcium and energy supplement and gentle lubrication of the vent may be useful. Physical manipulation of eggs and embryos is to be avoided as this commonly causes trauma and can result in oviduct rupture, oviduct prolapse and sudden death (Mader 2006; Mader and Divers 2013).

If this is not successful, then further treatment involves either surgical intervention or hormonal injections to induce oviposition or parturition. Surgical intervention involves laparotomy and hysterotomy to surgically relieve the dystocia. Attempts should be made at the time of surgery to identify the nature of the dystocia so that a prognosis for future breeding can be made. Hormonal treatments used to induce parturition or oviposition use either oxytocin or, preferably, arginine vasotocin. Oxytocin is of mammalian origin and has variable efficiency in different species of reptiles. It should not be used in obstructive dystocia as this will result in oviduct rupture. Arginine vasotocin is the natural oxytocin equivalent in reptiles and thus has better affinity for the reptile oviduct. However, it is more difficult to obtain. Both treatments should be used with caution as injections of oxytocin to induce oviposition in healthy tuatara have been shown to reduce egg and hatchling size (Nelson et al. 2004b), and premature injections of vasotocin are used to experimentally reduce brood size in reptiles (Bleu et al. 2013).

Complications of dystocia may include metritis (Sect. 8.2.6.1.2), yolk coelomitis and repeated dystocia due to oviduct adhesions and scarring (Mader 2006; Mader and Divers 2013).

8.2.6.2 Stomatitis

A common condition of captive reptiles is inflammation and infection of the oral cavity, known as stomatitis or mouth rot. This condition is associated with a diverse range of bacteria, protozoa and occasional fungi, especially *Candida* spp., that cause inflammation and ulceration of the tissues of the pharynx. Overseas, stomatitis has also been associated with viral disease and *Mycobacterium* spp. infection (Mehler and Bennett 2003), but these have not been reported in New Zealand. Stomatitis is particularly common in reptiles with disrupted emergence from hibernation/torpor due to widely varying temperature conditions. Inappropriate food items may cause gingivitis and lead to a wider stomatitis if untreated (Mehler and Bennett 2003).

Successful resolution of stomatitis involves identifying the responsible agents, cleaning and debriding the oral cavity with disinfectants and treating with the appropriate medication for the infectious agents involved. Stomatitis can be prevented by providing an appropriate diet and environmental conditions for the captive reptile (Mader 2006).

8.2.6.3 Dysecdysis

Dysecdysis is the term used to describe a failure of the normal skin moult in reptiles. The normal expected ecdysis (moulting pattern) of New Zealand reptiles is that geckos should shed the skin as a single piece, while skinks and tuatara shed their skin synchronously but in pieces. Tuatara are reported to shed once a year, over the course of a month (Blanchard 2002), while the other native reptiles appear to be more variable, though species-specific information is lacking. The frequency of ecdysis can be affected by the reptile's body condition and hydration and by environmental factors such as temperature, humidity and photoperiod. Some reptiles require surfaces to rub against to help remove old skin (Mader 2006). Young, rapidly growing reptiles are more likely to have more frequent periods of ecdysis.

In addition to the host and environmental factors listed above, overcrowding, stress and dermatitis due to bacteria, fungi and parasites have been implicated in dysecdysis. Old scars may also create focal points that prevent skin from shedding easily. The environmental factors most often associated with dysecdysis in captive reptiles are low temperatures and low humidity (Gartrell and Hare 2005; Mader 2006).

Dysecdysis can result in accumulations of old skin overlying new skin, and this can lead to secondary infections, especially with saprophytic fungi, or constrictions around extremities, particularly around the digits. These constrictions may result in loss of blood supply with accompanying avascular necrosis and osteomyelitis. The loss of digits, or even whole feet, is a common sequela of dysecdysis. Secondary infections often spread to cause fatal septicaemia or fungaemia in the reptiles (see Sect. 8.2.1 and 8.2.2) (Gartrell and Hare 2005; Mader 2006).

Another point of complication in ecdysis is the spectacle, which is a transparent scale of New Zealand geckos (and snakes) that covers the cornea (in the absence of eyelids) and a nictitating membrane. Lacrimal fluid lubricates and drains between the spectacle and cornea and loss of the spectacle will result in desiccation and scarring of the cornea. Dysecdysis can result in opaque retained spectacles over the eyes, which worsen with successive sheds. In geckos, dysecdysis has been associated with bacterial infections (Mader 2006).

The temptation to manually remove shedding skin should be resisted, as this may damage or even tear the underlying new skin. This is particularly true for retained spectacles since attempts at manual removal have previously resulted in ruptures of the underlying cornea and subsequent loss of the eye. Instead, it is best to assist a shed by soaking an animal daily in clean water and providing a humidity box, which is simply a hide box containing a substrate of wet sphagnum moss or vermiculite. Most animals in ecdysis will seek out the moisture. Usually, the provision of soaks, humidity boxes, substrate to rub against and good nutrition and husbandry will resolve the dysecdysis if it is uncomplicated by infection. The exception to this rule is in cases of digit constriction. If soaking does not rapidly resolve the ecdysis in these cases, careful incisions in the retained material may be necessary to restore blood flow. If the digits have undergone avascular necrosis, then amputation is required. Treatment of dysecdysis complicated by infection will usually require cultures and biopsies to isolate the organisms responsible followed by courses of the appropriate medications, including antiseptic soaks (Mader 2006).

8.3 Conclusion

Our knowledge of the diseases of New Zealand lizards is based largely upon information collected through passive surveillance of deaths in captivity or during translocations. More focused disease ecology studies are required, similar to those on tuatara and their parasites, to give us insights into the broader effects of disease in wild populations of reptiles. While the main causes of population decline in New Zealand lizards are undoubtedly habitat destruction and degradation, as well as the effects of introduced mammalian pest species, disease may become more important in fragmented populations and situations where lizards are intensively managed for conservation.

More research is required into the prevalence and taxonomy of reptile pathogens present in New Zealand, the effects of conservation efforts on host-parasite assemblages and the conservation of native parasites. Further work is needed to understand the effects of disturbances in the balance of host-parasite relationships on reptile health. Finally, the continued protection of New Zealand's native herpetofauna from exotic diseases is dependent on maintaining the existing ban on the importation of exotic reptiles and on strict border controls for the interception of accidentally introduced reptiles, their parasites and their pathogens.

References

Alexander S (2014) Treatment protocol for fungal disease in tuatara. Vetscript 27(8):25–27

Baling M, Ji W, Gartrell B, Brunton DH (2013) Detection of *Salmonella* during the translocation of two endemic New Zealand lizard species within the Hauraki Gulf. N Z J Zool 40(3): 249–254. doi:10.1080/03014223.2012.747970

Barry M, Peirce MA, Heath ACG, Brunton DH, Barraclough RK (2011) A new blood parasite within the relict endemic New Zealand gecko *Hoplodactylus duvaucelii*. Vet Parasitol 179(1–3):199–202. doi:10.1016/j.vetpar.2011.02.004

Blanchard B (2002) Tuatara husbandry manual. Department of Conservation, Wellington

Bleu J, Massot M, Haussy C, Meylan S (2013) An experimental study of the gestation costs in a viviparous lizard: a hormonal manipulation. Physiol Biochem Zool 86(6):690–701. doi:10.1086/673099

Broughton EI, Heffernan HM, Coles CL (2010) *Salmonella enterica* serotypes and antibiotic susceptibility in New Zealand, 2002–2007. Epidemiol Infect 138(3):322–329. doi:10.1017/S0950268809990458

Burgess TL, Gartrell BD, Blanchard B (2009) A survey of the husbandry of captive tuatara (*Sphenodon* spp.) in relation to factors implicated in nutritional secondary hyperparathyroidism. N Z Vet J 57(6):378–382

Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). Mol Phylogenet Evol 52(2):470–487. doi:10.1016/j.ympev.2009.03.021

Chapple DG, Bell TP, Chapple SNJ, Miller KA, Daugherty CH, Patterson GB (2011) Phylogeography and taxonomic revision of the New Zealand cryptic skink (Oligosoma inconspicuum; Reptilia: Scincidae) species complex. Zootaxa 2782:1–33

Chapple DG, Knegtmans J, Kikillus H, van Winkel D (2016) Biosecurity of exotic reptiles and amphibians in New Zealand: building upon Tony Whitaker's legacy. J R Soc N Z 46:66–84. doi:10.1080/03036758.2015.1108344

Colenso RW (1879) Notes and observations on the animal economy and habits of one of our New Zealand lizards, supposed to be a new species of Naultinus. Trans R Soc NZ 12:251–264

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Cui B, Fu Q, Liu L, Li W-J (2009) UV radiation-induced cataract model in rats. Int J Ophthalmol 9(5):836–838

Divers SJ, Cooper JE (2000) Reptile hepatic lipidosis. Semin Avian Exot Pet Med 9(3):153–164. doi:10.1053/ax.2000.7136

Freeman AB, Hickling GJ, Bannock CA (1996) Response of the skink *Oligosoma maccanni* (Reptilia: Lacertilia) to two vertebrate pest-control baits. Wildl Res 23(4):511–516

Gartrell BD, Hare KM (2005) Mycotic dermatitis with digital gangrene and osteomyelitis, and protozoal intestinal parasitism in Marlborough green geckos (Naultinus manukanus). N Z Vet J 53(5):363–367

Gartrell BD, Jillings E, Adlington BA, Mack H, Nelson NJ (2006) Health screening for a translocation of captive-reared tuatara (*Sphenodon punctatus*) to an island refuge. N Z Vet J 54(6):344–349

Gartrell BD, Youl JM, King CM, Bolotovski I, McDonald WL, Nelson NJ (2007) Failure to detect *Salmonella* species in a population of wild tuatara (*Sphenodon punctatus*). N Z Vet J 55(3): 134–136

Godfrey SS, Bull CM, Nelson NJ (2008) Seasonal and spatial dynamics of ectoparasite infestation of a threatened reptile, the tuatara (Sphenodon punctatus). Med Vet Entomol 22(4):374–385. doi:10.1111/j.1365-2915.2008.00751.x

Godfrey SS, Moore JA, Nelson NJ, Bull CM (2010a) Social network structure and parasite infection patterns in a territorial reptile, the tuatara (*Sphenodon punctatus*). Int J Parasitol 40(13):1575–1585. doi:10.1016/j.ijpara.2010.06.002

Godfrey SS, Moore JA, Nelson NJ, Bull CM (2010b) Unravelling causality from correlations: revealing the impacts of endemic ectoparasites on a protected species (tuatara). Parasitology 137(2):275–286. doi:10.1017/S0031182009991314

Godfrey SS, Nelson NJ, Bull CM (2011a) Ecology and dynamics of the blood parasite, *Hepatozoon tuatarae* (Apicomplexa), in tuatara (*Sphenodon punctatus*) on Stephens Island, New Zealand. J Wildl Dis 47(1):126–139

Godfrey SS, Nelson NJ, Bull CM (2011b) Microhabitat choice and host-seeking behaviour of the tuatara tick, *Amblyomma sphenodonti* (Acari: Ixodidae). N Z J Ecol 35(1):52–60

Gómez A, Nichols E (2013) Neglected wild life: parasitic biodiversity as a conservation target. Int J Parasitol Parasites Wildl 2(1):222–227. doi:10.1016/j.ijppaw.2013.07.002

Hare KM, Cree A (2016) Thermal and metabolic physiology of New Zealand lizards. Chap. 9. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Heath ACG, Bishop DM (2006) Flystrike in New Zealand: an overview based on a 16-year study, following the introduction and dispersal of the Australian sheep blowfly, *Lucilia cuprina* Wiedemann (Diptera: Calliphoridae). Vet Parasitol 137(3–4):333–344

Heath ACG, Whitaker AH (2015) Mites (Acari: Pterygosomatidae, Macronyssidae) taken from lizards intercepted at the New Zealand border. Syst Appl Acarol 20(7):739–756. doi:10.11158/saa.20.7.3

Hellebuyck T, Pasmans F, Haesebrouck F, Martel A (2012) Dermatological diseases in lizards. Vet J 193(1):38–45. doi:10.1016/j.tvjl.2012.02.001

Herbert JDK, Godfrey SS, Bull CM, Menz RI (2010) Developmental stages and molecular phylogeny of *Hepatozoon tuatarae*, a parasite infecting the New Zealand tuatara, *Sphenodon punctatus* and the tick, *Amblyomma sphenodonti*. Int J Parasitol 40(11):1311–1315. doi:10.1016/j.ijpara.2010.03.018

Hitchmough R, Barr B, Lettink M, Monks J, Reardon JT, Tocher M, van Winkel D, Rolfe J (2016) Conservation status of New Zealand reptiles, 2015. Department of Conservation, Wellington

Hoare JM, Hare KM (2006) The impact of brodifacoum on non-target wildlife: gaps in knowledge. N Z J Ecol 30(2):157–167

Julian AF, Durham PJK (1982) Adenoviral hepatitis in a female bearded dragon (*Amphibolurus barbatus*). N Z Vet J 30(5):59–60. doi:10.1080/00480169.1982.34880

Keall SN, Nelson NJ, Daugherty CH (2010) Securing the future of threatened tuatara populations with artificial incubation. Herpetol Conserv Biol 5(3):555–562

Kikillus KH, Gartrell BD, Motion E (2011) Prevalence of *Salmonella* spp., and serovars isolated from captive exotic reptiles in New Zealand. N Z Vet J 59(4):174–178. doi:10.1080/00480169.2011.579246

Kohler G (2005) Incubation of reptile eggs. Krieger Publishing, Malabar, FL

Latney LV, Wellehan J (2013) Selected emerging infectious diseases of Squamata. Vet Clin North Am Exot Anim Pract 16(2):319–338. doi:10.1016/j.cvex.2013.01.003

Le Souëf AT, Barry M, Brunton DH, Jakob-Hoff R, Jackson B (2015) Ovariectomy as treatment for ovarian bacterial granulomas in a Duvaucel's gecko (*Hoplodactylus duvaucelii*). N Z Vet J 63(6):340–344. doi:10.1080/00480169.2015.1063468

Liggins L, Chapple DG, Daugherty CH, Ritchie PA (2008) A SINE of restricted gene flow across the Alpine Fault: phylogeography of the New Zealand common skink (Oligosoma nigriplantare polychroma). Mol Ecol 17:3668–3683

Mader DR (ed) (2006) Reptile medicine and surgery, 2nd edn. Saunders Elsevier, St Louis, MO

Mader DR, Divers SJ (eds) (2013) Current therapy in reptile medicine and surgery. Saunders Elsevier, St Louis, MO

Maria L (2014) Interceptions of reptiles and amphibians. Surveillance 41(4):21–22

McKenna PB (2003) An annotated checklist of ecto- and endoparasites of New Zealand reptiles. Surveillance 30(3):18–25

Mehler SJ, Bennett RA (2003) Oral, dental, and beak disorders of reptiles. Vet Clin North Am Exot Anim Pract 6(3):477–503. doi:10.1016/S1094-9194(03)00032-X

Middleton DMRL, Minot EO, Gartrell BD (2010) *Salmonella enterica* serovars in lizards of New Zealand's offshore islands. N Z J Ecol 34(2):247–252

Middleton DMRL, La Flamme AC, Gartrell BD, Nelson NJ (2014) Reptile reservoirs and seasonal variation in the environmental presence of *Salmonella* in an island ecosystem, Stephens Island, New Zealand. J Wildl Dis 50(3):655–659. doi:10.7589/2013-10-277

Middleton DMRL, Nelson NJ, Gartrell BD, La Flamme AC (2015) Presence of antibodies to Salmonella in tuatara (*Sphenodon punctatus*) sera. Comp Immunol Microbiol Infect Dis 41: 17–27. doi:10.1016/j.cimid.2015.06.001

Mitchell MA, Diaz-Figueroa O (2004) Wound management in reptiles. Vet Clin North Am Exot Anim Pract 7(1):123–140

Mockett ST (2015) The evolution and diversity of parasites of New Zealand lizards. University of Otago, Dunedin

Nelson NJ, Thompson MB, Pledger S, Keall SN, Daugherty CH (2004a) Egg mass determines hatchling size, and incubation temperature influences post-hatching growth, of tuatara *Sphenodon punctatus*. J Zool 263(1):77–87. doi:10.1017/S095283690400490X

Nelson NJ, Thompson MB, Pledger S, Keall SN, Daugherty CH (2004b) Induction of oviposition produces smaller eggs in tuatara (*Sphenodon punctatus*). N Z J Zool 31(4):283–289

Nelson NJ, Moore JA, Pillai S, Keall SN (2010) Thermosensitive period for sex determination in the Tuatara. Herpetol Conserv Biol 5(2):324–329

Nielsen SV, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol 59(1):1–22. doi:10.1016/j.ympev.2010.12.007

Paré JA (2013) Update on fungal infections in reptiles. In: Mader DR, Divers SJ (eds) Current therapy in reptile medicine and surgery. Saunders Elsevier, St Louis, MO, pp 53–56. doi:10.1016/B978-1-4557-0893-2.00006-5

Peveling R, Demba SA (2003) Toxicity and pathogenicity of *Metarhizium anisopliae* var. *acridum* (Deuteromycotina, Hyphomycetes) and fipronil to the fringe-toed lizard *Acanthodactylus dumerili* (Squamata: Lacertidae). Environ Toxicol Chem 22(7):1437–1447. doi:10.1897/1551-5028(2003)22<1437:TAPOMA>2.0.CO;2

Poulin R (2014) Parasite biodiversity revisited: frontiers and constraints. Int J Parasitol 44(9): 581–589. doi:10.1016/j.ijpara.2014.02.003

Raidal SR, Ohara M, Hobbs RP, Prince RIT (1998) Gram-negative bacterial infections and cardiovascular parasitism in green sea turtles (*Chelonia mydas*). Aust Vet J 76(6):415–417

Raske M, Lewbart GA, Dombrowski DS, Hale P, Correa M, Christian LS (2012) Body temperatures of selected amphibian and reptile species. J Zoo Wildl Med 43(3):517–521. doi:10.1638/2011-0244R.1

Reardon JT, Norbury G (2004) Ectoparasite and hemoparasite infection in a diverse temperate lizard assemblage at Macraes Flat, South Island, New Zealand. J Parasitol 90(6):1274–1278. doi:10.1645/GE-3326

Sigler L, Hambleton S, Paré JA (2013) Molecular characterization of reptile pathogens currently known as members of the *Chrysosporium* anamorph of *Nannizziopsis vriesii* complex and relationship with some human-associated isolates. J Clin Microbiol 51(10):3338–3357. doi:10.1128/JCM.01465-13

Simpson M (2006) Hepatic lipidosis in a Black-Headed Python (*Aspidites melanocephalus*). Vet Clin North Am Exot Anim Pract 9(3):589–598. doi:10.1016/j.cvex.2006.05.013

Stringer AP, Linklater W (2014) Everything in moderation: principles of parasite control for wildlife conservation. BioScience 64(10):932–937. doi:10.1093/biosci/biu135

Thompson MB (1990) Incubation of eggs of tuatara, *Sphenodon punctatus*. J Zool 222(2):303–318

van Andel M, Jackson BH, Midwinter AC, Alley MR, Ewen JG, McInnes K, Jakob Hoff R, Reynolds AD, French N (2015) Investigation of mortalities associated with *Salmonella* spp. infection in wildlife on Tiritiri Matangi Island in the Hauraki Gulf of New Zealand. N Z Vet J 63(4):235–239. doi:10.1080/00480169.2014.990065

Wada S, Kawano-Yamashita E, Koyanagi M, Terakita A (2012) Expression of UV-sensitive parapinopsin in the iguana parietal eyes and its implication in UV-sensitivity in vertebrate pineal-related organs. PLoS One 7(6):e39003. doi:10.1371/journal.pone.0039003

Warwick C (1991) Observations on disease-associated preferred body temperatures in reptiles. Appl Anim Behav Sci 28(4):375–380. doi:10.1016/0168-1591(91)90169-X

Wedding CJ, Ji W, Brunton DH (2010) Implications of visitations by Shore Skinks *Oligosoma smithi* to bait stations containing brodifacoum in a dune system in New Zealand. Pac Conserv Biol 16(2):86–91

Youl JM (2006) Fipronil use in Grand skinks (*Oligosoma grande*). Massey University, Report to the Department of Conservation

Chapter 9

Thermal and Metabolic Physiology of New Zealand Lizards

Kelly M. Hare and Alison Cree

Abstract New Zealand's endemic lizards have speciated to fill nearly every available habitat type, and many species inhabit areas with low environmental temperatures. Unusually, from a global perspective, both lineages (geckos and skinks) include diurnally foraging and nocturnally foraging species. We review their physiology, focusing mainly on thermal and metabolic studies. Species that bask avidly, and those that bask cryptically, have field body temperatures (T_b) averaging about 17–25 °C on spring or summer days, with no individuals known to voluntarily exceed 34 °C. Thermal performance curves for sprint speed have a typical asymmetric shape but are 'left shifted' compared with many species overseas. In particular, critical minimum and selected temperatures are relatively low, as expected for high-latitude species, and geckos have particularly left-shifted curves. Warm daytime temperatures enhance many physiological functions, including embryonic development and digestion. In general, metabolic rate also increases with T_b, and metabolism alters (with no discernible pattern) in response to different acclimation temperatures. However, many species show thermal independence of metabolic rate over some range of temperatures, suggesting high metabolic stability; a relatively wide performance breadth also occurs in sprint speed. Nocturnally foraging species, which voluntarily emerge at low T_b (sometimes ≤ 10 °C), have physiological adaptations that enhance performance, including a low energetic cost of locomotion, but may have relatively high rates of cutaneous water loss. As a group, New Zealand's lizards function well at low temperatures, and the warmer temperatures that climate change will bring may enhance some aspects of their physiological function.

Keywords Acclimation • Cost of locomotion • Critical thermal maximum • Critical thermal minimum • Evaporative water loss • Metabolic rate • Oxygen

---

K.M. Hare (✉)
Centre for Biodiversity and Restoration Ecology, Victoria University of Wellington,
Wellington, New Zealand
e-mail: kelly.hare@gmail.com

A. Cree
Department of Zoology, University of Otago, Dunedin, New Zealand

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_9

consumption • Sprint speed • Thermal performance • Thermal preference • Thermal tolerance

9.1 Introduction

Virtually all biological processes of reptiles are sensitive to temperature. At the cellular level, biochemical reaction rates increase (sometimes geometrically) with increasing temperature, reaching a maximum at some optimal temperature, and decreasing quickly at higher temperatures. Most biological processes at the whole-organism level, including rates of locomotion, growth and development, follow the same pattern (see review in Kingsolver 2009). Thus, many physiological studies of reptiles directly or indirectly involve responses to environmental temperature, meaning that researchers may need to control for temperature differences to enable broader evolutionary questions to be addressed. In fact, data on physiology are relevant to all branches of biology, including conservation. For example, physiological constraints strongly influence the distribution of animals, including the microenvironment in which animals persist (Neilson 2002). Understanding a species' physiology can therefore assist conservation by, for example, enabling predictions of vulnerability to disturbance, predicting potential search areas for rare and threatened species (Neilson 2002), enhancing monitoring methods (Thierry et al. 2009; Lettink and Hare 2016) and providing guidelines for captive husbandry (Gibson 2016).

This chapter examines the thermal and metabolic physiology of New Zealand's lizards, as well as the limited information available for patterns of water loss. In particular, we examine the following questions. (1) How does body temperature affect whole-animal performance, metabolic rate and water loss? (2) What factors need to be controlled for when examining these physiological patterns? For example, does seasonal acclimatisation (in the field) or acclimation to different levels of temperature or moisture (in the laboratory) alter the physiological responses of individuals to body temperature? (3) Are there obvious differences in responses between the two main lineages (diplodactylid geckos vs. skinks), or between species that forage diurnally compared with those that forage nocturnally? From answers to these questions, we draw general conclusions about the extent to which New Zealand lizards have, through evolutionary change, become 'cold adapted' in their physiological responses. We also make some comparisons with New Zealand's only non-squamate lepidosaur, the rhynchocephalian tuatara (*Sphenodon punctatus*), and comment on some possible implications of climate change.

New Zealand lizards inhabit a landscape that extends to high latitudes and is never far from the coast (Chapple and Hitchmough 2016). Thus, conditions are often relatively cool and stable compared with the habitats of many well-studied lizards overseas. Both main lineages also have a high proportion of species that exhibit nocturnal activity (see Hare et al. 2016). Although the daily activity patterns of lizards have often been classified in a dichotomous way (diurnal vs. nocturnal, sometimes including crepuscular), these terms do not do justice to the activity patterns of many lizards, including those in New Zealand. In particular, many lizards that forage nocturnally also bask, although this activity may not often be seen by humans unless cameras or other recording devices are used (Gibson et al. 2015; Lettink and Hare 2016). Nonetheless, the capacity for nocturnal activity in ectotherms, such as lizards, raises a paradox: nocturnally active lizards operate at temperatures that are suboptimal for locomotion and much lower than the temperatures these lizards choose when warmer temperatures are available (see Autumn et al. 1994). We therefore explore the physiological mechanisms that enable nocturnally foraging lizards to overcome the 'handicap' of activity at low temperatures, and whether these traits extend to New Zealand's other cold-active lizards.

9.2 Thermal Performance Curves, Thermal Tolerance and Thermal Preference

Environmental conditions profoundly influence the lives of lizards. For example, the endangered skinks *Oligosoma grande* and *O. otagense*, two rock-dwelling heliotherms (avid sun baskers) at Macraes Flat, Otago, are rarely if ever seen emerged in summer if shade air temperature (T_a; see Table 9.1 for list of abbreviations) is less than 7 °C. However, on warmer days the number of emerged individuals increases significantly up to at least ~24 °C (Coddington and Cree 1997). Thus, the influence of T_a (or rock temperature) on emergence, in conjunction with other climate variables including cloud cover and wind speed, must be understood when designing survey techniques for these and other lizards.

Environmental temperatures, cloud cover and wind speed influence emergence because of (1) their strong influence on the body temperature (T_b) that basking lizards can attain and (2) the resulting influence of T_b on performance. For example, McCann's skinks (*O. maccanni*, another diurnal, viviparous heliotherm from Macraes Flat; Fig. 9.1a) emerge at low T_a of between 7.7 and 10.3 °C in the field (as low as 5 °C in the laboratory; Vermunt et al. 2014) and rapidly attain field T_bs up to 17.3 °C warmer than T_a (Fig. 9.1b; Hare et al. 2009). The difference between T_a and T_b is greatest when conditions are sunny (hence more radiation absorbed) and wind speed is low (hence lower convective losses). As in other lizards, the effect of the T_b attained on whole-animal performance can readily be assessed in the laboratory by measuring sprint speed (Huey 1982; Angilletta 2009). The thermal performance curve for sprint speed in *O. maccanni* shows the expected asymmetric shape for ectotherms, increasingly gradually to a peak beyond which it more rapidly declines (Angilletta 2009; Kingsolver 2009; Huey et al. 2012; Fig. 9.1c). Speed increases more than threefold with T_b over the range 5–25 °C, reaching a plateau between 25 and 32 °C within which speed (~0.8 m s^{-1}) does not vary statistically

Table 9.1 Abbreviations as used in the text

Acronym	Term	Definition
C_{min}	Energetic cost of locomotion	A dimensionless ratio defined as the rate of energy consumption divided by an individual's mass and speed; here, calculated by measuring rate of oxygen consumption during progressively faster speeds during steady exercise on a treadmill
CT_{max}	Critical thermal maximum	The upper body temperature at which the righting response is lost after warming at a constant rate
CT_{min}	Critical thermal minimum	The lower body temperature at which the righting response is lost after cooling at a constant rate
CWL	Cutaneous water loss	Measurement of water loss through the skin (in mg H_2O g body mass^{-1} h^{-1})
EWL	Evaporative water loss	The combination of rates of cutaneous water loss and respiratory water loss (in mg H_2O g body mass^{-1} h^{-1})
MR	Metabolic rate	Rate of oxygen consumption (in mL O_2 g^{-1} h^{-1}) or carbon dioxide production (in mL CO_2 g^{-1} h^{-1})
Q_{10}	Temperature coefficient $Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2 - T_1}\right)}$	Represents the thermal sensitivity, or the factor by which the rate (R) of a reaction changes for every 10° in temperature (T; in °C or °F); R_1 is the measured reaction rate at temperature T_1 (where $T_1 < T_2$), and R_2 is the measured reaction rate at temperature T_2. A Q_{10} of 1 indicates no change in rate over 10 °C; a Q_{10} of 2 indicates a doubling of rate over 10 °C
rh	Relative humidity	The current absolute humidity relative to the maximum (highest possible) for that temperature; expressed as a percentage
T_{a}	Air temperature	Temperature of air measured in the shade ~ 1 m from the ground
T_{b}	Body temperature	Temperature of the body (usually measured within the cloaca)
T_{p}	Preferred temperature	See selected temperature
T_{sel}	Selected temperature	The body temperature as selected on a thermal gradient (also known as preferred temperature)
TSM	Thermal safety margin	The difference between current mean T_{sel} and the mean T_{a} (mean temperature of warmest quarter of the year, from http://www.worldclim.org/bioclim)

(Gaby et al. 2011). This plateau is interpreted as the optimal temperature range for sprinting (Gaby et al. 2011).

Sprint speed in *O. maccanni* must plummet rapidly at temperatures only slightly higher than this plateau. At Macraes Flat, these skinks retreat to shade to avoid T_{b} above 32–33 °C (Table 9.2; Hare et al. 2009). In the laboratory, lethal temperatures are only slightly higher in *Oligosoma* spp. ([as *Leiolopisma zelandica*], probably *O. maccanni*/*O. polychroma*). For example, summer-acclimatised or warm-acclimated skinks tolerated being at 35 °C for 24 h (with escape attempts), those at 37.5 °C survived only 2–8 h, and those at 40 °C survived only 15–50 min (Cook 1969; Morris 1974, 1984; the lethal temperature was ~3 °C lower in winter-acclimatised animals). More recent studies on lizards have favoured measuring

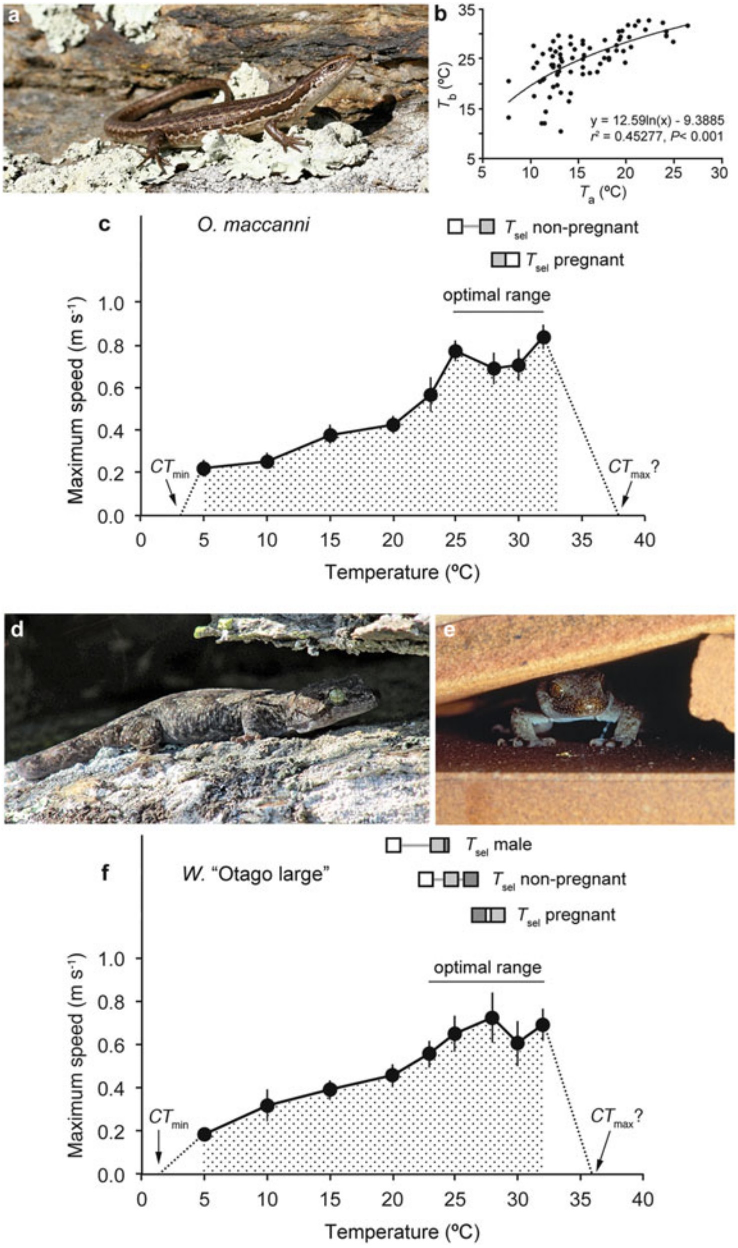


Fig. 9.1 Thermal behaviour and thermal performance curves for two lizards from Macraes Flat: the skink *Oligosoma maccanni* (**a–c**), a diurnal heliotherm, and *Woodworthia* 'Otago large' (**d–f**), a nocturnally foraging gecko that basks cryptically. *O. maccanni* panel: (**a**) basking (photo: ©A. Cree). (**b**) Relationship between air temperature (T_a) and body temperature (T_b) when basking is possible. Data redrawn (pooled for pregnant and non-pregnant skinks, as slopes and intercepts did not differ) from Hare et al. (2009). (**c**) Thermal performance curve for sprint speed in non-pregnant *O. maccanni* (*black dots*, mean ± SE from Gaby et al. 2011); optimal range is where mean values do not differ significantly. Value for CT_{min} from Besson and Cree (2011). Value for CT_{max} inferred

the critical thermal maximum (CT_{max}, often survivable) as an upper extreme; this involves heating the animals at a constant rate until the righting response is lost or onset of spasms occurs (Lutterschmidt and Hutchison 1997). Although CT_{max} has not been measured for *O. maccanni*, in other heliothermic lizards, it averages about 6.4 °C above the upper limit for field activity (Huey 1982). From field T_{b} and lethal temperature data, we infer that CT_{max} in *O. maccanni* is ~37–39 °C in summer. At the opposite end of the thermal performance curve, loss of righting ability after cooling at a standard rate is recognised as the critical thermal minimum (CT_{min}). The CT_{min} for *O. maccanni* is 3.3 °C (Besson and Cree 2011), although as with CT_{max} this value may vary depending on acclimatisation, acclimation or cooling/heating rate.

Another parameter relevant to thermal physiology is selected or preferred body temperature (T_{sel} or T_{p}): the T_{b} chosen on a thermal gradient without the influence of abiotic or biotic variables that might affect microhabitat use. Pregnant, field-fresh *O. maccanni* have a mean daytime T_{sel} of 28.9 °C averaged between 1000 and 1500 h (Fig. 9.1c; Hare et al. 2009). Thus, T_{sel} lies, as expected, within the optimal range for sprinting. Equivalent values in non-pregnant females after prolonged captivity are lower and more variable (~26 °C), but whether these differences are due to reproductive state or time in captivity is unknown (Besson and Cree 2011; see also Thierry et al. 2009).

Physiological processes other than sprint speed are also influenced by T_{b}, but may show slightly different relationships. For example, in *O. maccanni* feeding and digestion cease between 12 and 5 °C (Besson and Cree 2011). Embryonic

Fig. 9.1 (continued) from lethal temperatures for small *Oligosoma* (probably *O. maccanni*/*O. polychroma*) from Otago and Canterbury [data from Cook (1969) and Morris (1974, 1984)]. Activity temperature range (*stipple*) is from field and laboratory data (Hare et al. 2009; Vermunt et al. 2014). Selected temperatures (T_{sel}) are means for 1000 h (*open square*) and 1500 h (*light-grey square*) for field-fresh pregnant females in spring (Hare et al. 2009) and for non-pregnant females acclimatised to summer conditions in the laboratory (Besson and Cree 2011). *W.* 'Otago large' panel**:** (**d**) A female basking at a crevice entrance (photo: ©Georgia Moore). (**e**) A female standing on toes in a laboratory retreat to warm its dorsum by contact with a ceramic tile heated from above (photo: ©Jennifer Rock). (**f**) Thermal performance curve for sprint speed in non-pregnant *W.* 'Otago large' (Gaby et al. 2011). Value for CT_{min} from Besson and Cree (2011). Value for CT_{max} inferred from lethal temperatures for *W.* 'Central Otago' (Cook 1969). Activity temperature range from sources in Table 9.2, Vermunt et al. (2014) and unpubl. obs. Selected temperatures are means for 1000 h (*open square*), 1400 h (*light-grey square*) and 1700 h (*dark-grey square*) for field-fresh geckos in mid-summer (Rock et al. 2000). T_{b} vs. T_{a} data for *O. maccanni* reprinted with permission from Hare et al. (2009), Copyright ©John Wiley & Sons, Inc., 2009 [Modified from Hare et al. (2009), Modelling exposure to selected temperature during pregnancy: the limitations of squamate viviparity in a cool-climate environment, 96:541–552, Fig. 4b. Copyright ©2009 by the Biological Journal of the Linnean Society. Reprinted by permission of John Wiley & Sons, Inc.]. Sprint-speed data are reprinted with permission from Gaby et al. (2011), Copyright ©Springer 2011 [Reprinted from Gaby et al. (2011), Thermal dependence of locomotor performance in two cool-temperate lizards, 197:869–875, Fig. 2a, b. Copyright ©2011 by the Journal of Comparative Physiology A. Copyright (2011) with permission from Springer.]

development is also temperature dependent and, as with digestion, probably requires relatively warm temperatures: reduced maternal access to basking opportunity (e.g., access to T_{sel} for 28 h week^{-1} rather than 40–56 h week^{-1}) increases gestation length and lowers pregnancy success in *O. maccanni* (Cree and Hare 2010). A lower thermal limit for embryonic development in *O. maccanni* has not been established, but research on Australian lizards, the oviparous New Zealand skink *O. suteri* and oviparous tuatara (*S. punctatus*), suggests that constant temperatures below ~16 °C are unlikely to support successful development (Hare et al. 2009 and references therein).

Another viviparous lizard from Macraes Flat that provides a contrast in daily activity pattern to *O. maccanni* is the nocturnally foraging gecko *Woodworthia* 'Otago large' (also known as *W.* 'Otago/Southland'; Nielsen et al. 2011). In the warmer months, wild individuals leave their rocky retreats to forage nocturnally at T_{b} at least as low as 13 °C (Table 9.2; 5 °C in the laboratory; Vermunt et al. 2014). They also bask by day close to retreat sites (Fig. 9.1d); remote cameras confirm up to 5.5 h basking (in an 8 h filming day), with females basking more than males (Gibson et al. 2015). In the laboratory, pregnant females bask more than males or non-pregnant females (Cree et al., unpublished). Geckos that remain under warm, thin rocks on warm days are not 'inactive'; they adjust their positions and postures to maximise heat gain from above and minimise loss below (Fig. 9.1e; Rock et al. 2002). By engaging in daytime thermoregulatory activities, geckos attain warm field T_{b}s up to ~32–33 °C and appear to avoid warmer T_{b}s on hot afternoons by shifting to deeper crevices (Rock and Cree 2008; Cree, unpublished). Thus, these geckos achieve similar field T_{b} on sunny days to *O. maccanni* (albeit probably slightly less rapidly), and suggestions that they are thermoconformers (Spencer and Grimmond 1994) are inaccurate.

As in *O. maccanni*, sprint speed in *W.* 'Otago large' increases significantly over the range 5–25 °C, with a wide plateau (the optimal temperature range) between 23 and 32 °C (Fig. 9.1f; Gaby et al. 2011). The CT_{max} has not been measured, but studies on lethal temperatures in the gecko *W.* 'Central Otago' suggest that CT_{max} is lower than in *Oligosoma* spp. (Cook 1969); we epredict it as between 35 and 37 °C in *W.* 'Otago large'. Mean CT_{min} of *W.* 'Otago large' is $\leq$1.2 °C (Besson and Cree 2011), about 2 °C lower than in *O. maccanni.*

Thermal preference in *W.* 'Otago large' from Macraes Flat varies greatly with season, sex, pregnancy status and time of day; mean daytime values for field-fresh geckos are highest (~28 °C) in females during mid-pregnancy (Fig. 9.1f; Rock et al. 2000). Corresponding values for non-pregnant females and males vary more with time of day, averaging ~25 °C and 23 °C, respectively (Fig. 9.1f; Rock et al. 2000; Besson and Cree 2011). Compared with *O. maccanni*, feeding and digestion are less impaired by cool temperature (Besson and Cree 2011), and embryonic development under low maternal basking opportunity is more successful (Cree and Hare 2010).

Intriguing relationships between T_{b} and plasma concentrations of the adrenal glucocorticoid hormone corticosterone have been observed in *W.* 'Otago large' (Girling and Cree 1995; Cree et al. 2003). Although corticosterone is a hormone released during acute stress response (e.g. following capture and confinement), it plays a role in normal carbohydrate metabolism, and the positive relationship between T_b and baseline corticosterone in *W*. 'Otago large' may simply reflect the normal increase in metabolic activity that occurs at warm temperatures (Cree et al. 2003). If administered using implants, exogenous corticosterone can induce increased basking and/or increased T_sel in these geckos (Cree et al. 2003; Preest and Cree 2008), indicating complex interrelationships between T_b and adrenal function. Whether progesterone, a hormone more closely associated with pregnancy in lizards (Cree and Hare 2016), also induces basking behaviour in these geckos is unknown.

We now compare thermal parameters in *O. maccanni* and *W*. 'Otago large' from Macraes Flat with the limited data available for New Zealand lizards from other locations. Field T_b values recorded in spring and summer by day for species from mid-low elevations are broadly similar (Table 9.2). For example, mean field T_b during spring and summer (without control for T_a, and on the sometimes non-random days when herpetologists choose to do fieldwork) typically falls within about 17–25 °C, regardless of whether species are diurnal baskers (*Naultinus* geckos and some *Oligosoma* skinks), secretive and/or crepuscular (some *Oligosoma*), or nocturnally foraging geckos (*Woodworthia* spp.; *Hoplodactylus duvaucelii*). Maximum individual values also appear consistent; no New Zealand lizard is known to voluntarily exceed a field T_b of 34 °C. In *O. lineoocellatum*, a T_b of 35 °C for 7 h was sometimes lethal (Morris 1971). Low CT_min values have been observed in a few other *Woodworthia* species (~0.3–1.9 °C; Tocher 1993) and *N. gemmeus* (~1.0 °C; Besson and Cree 2011), and possibly *O. lineoocellatum* (Morris 1971). Mean T_sel by day in non-pregnant females and males of other *Woodworthia* species varies between about 19–28 °C depending on season, time of day and acclimation conditions (Tocher 1992; Rock et al. 2000); these values, and those in non-pregnant *N. gemmeus* (~21–27 °C: Besson and Cree 2011), are comparable with equivalent groups in *W*. 'Otago large', but we know of no data for skinks other than *O. maccanni*. Body temperature (within the range ~5–32 °C) has a similar positive influence on sprint speed in *O. infrapunctatum* and *O. lineoocellatum* (Duncan 1999) to that in *O. maccanni*.

One area in which small skinks (probably *O. maccanni*/*O. polychroma*, from coastal Canterbury) have received closer attention than geckos is their ability to tolerate sub-zero temperatures. These skinks apparently tolerate some degree of freezing without supercooling for several minutes, as well as supercooling to −5 °C for several hours, although they do not survive the spontaneous crystallisation that results from supercooling to −6 °C (Morris 1974). Some nocturnally foraging geckos live in high-latitude and/or high-elevation (alpine) areas of southern New Zealand with very low T_a and have an impressive ability for emergence at extremely low T_a in captivity (~3–7 °C: e.g., Whitaker 1984; Jewell 1997). These geckos (and the diurnal skinks with which they are sympatric) might have even better supercooling capacities than skinks from warmer locations. However, details of thermal biology for these inaccessible species, and for lizards from the other climate extreme of New Zealand (the subtropics), are lacking.

Table 9.2 Field body temperatures (T_b; mean ± SE with range in parentheses) reported for New Zealand lizards during spring or summer

Species	Location and region	Latitude (°S)	Daily foraging period	Month/ season	Repro. group	T_b (°C)	*N*	Time of day and comments on location/ activity	Source
Geckos									
Hoplodactylus duvaucelii	Korapuki I, Mercury Is, Waikato	36° 40′	N (b)	Spring	ND	20.4 ± 0.6 (ND)	4 groups	By day, aggregated in ‘shelters’	Barry et al. (2014)
Hoplodactylus duvaucelii	Korapuki I, Mercury Is, Waikato	36° 40′	N (b)	Summer	ND	25.0 ± 0.5 (≤26.6)	4 groups	By day, aggregated in ‘shelters’	Barry et al. (2014)
Hoplodactylus duvaucelii	South Trio I, Marlborough Sounds	40° 52′	N (b)	*Nov*	*ND*	*16.8 ± 0.1 (16.7–17.0)*	*5*	*By night; emerged*	Werner and Whitaker (1978)
Hoplodactylus duvaucelii	North Brother I, Marlborough Sounds	41° 07′	N (b)	*ND*	*ND*	*ND (as low as 8)*	*ND*	*By night; actively foraging*	Barwick (1982)
Naultinus gemmeus	Otago Peninsula, Otago	45° 50′	D	Oct–Dec	Mixed	ND (~11–30)	26	By day, in foliage; many basking	Salmon (2002)
N. manukanus	Stephens I, Marlborough Sounds	40° 42′	D	Nov	ND	23.8 ± ND (16.5–31.1)	25	By day, in foliage; most basking	Werner and Whitaker (1978)
N. stellatus	St Arnaud, Nelson	41° 48′	D	Nov	ND	22.9 ± 3.0 (18.3–28.5)	3	By day, in foliage; all basking	Werner and Whitaker (1978)
N. rudis	Conical Hill, Hanmer	42° 31′	D	Nov	ND	ND (29.5)	1	By day, in foliage; basking	Werner and Whitaker (1978)
[a]*Woodworthia* cf. *brunnea*	Motunau Island, Canterbury	43° 04′	N (b)	Nov	F	22.6 ± ND (~16.0–29.0)	29	By day; under stones, logs, etc.; T_b up to ~13 °C above T_a and warmer than for males	Werner and Whitaker (1978)

(continued)

Table 9.2 (continued)

Species	Location and region	Latitude (°S)	Daily foraging period	Month/ season	Repro. group	T_b (°C)	*N*	Time of day and comments on location/ activity	Source
[a]*Woodworthia* cf. *brunnea*	Motunau Island, Canterbury	43° 04′	N (b)	Nov	M	20.6 ± ND (~15.0–26.0)	29	By day; under stones, logs, etc.; T_b up to ~11 °C above T_a and cooler than for females	Werner and Whitaker (1978)
[a]*Woodworthia* cf. *brunnea*	Motunau Island, Canterbury	43° 04′	N (b)	Nov	*ND*	*ND (10.0–13.0)*	*15*	*By night, emerged*	Werner and Whitaker (1978)
[a]*Woodworthia* cf. *brunnea*	Kaitorete Spit, Canterbury	43° 49′	N (b)	Nov	ND	28.1 ± 1.0 (26.1–32.0)	5	On hot day; warmest gecko in sun	Morris (1971)
W. chrysosiretica	Mana Island, Wellington	41° 40′	N (b)	Nov	PF	20.3 ± 0.8 (17.0–27.9)	14	By day, emerged on vegetation; T_b warmer than T_a and not different from males	Hare (2007)
W. chrysosiretica	Mana Island, Wellington	41° 40′	N (b)	Nov	M	22.2 ± 1.6 (18.2–27.1)	6	By day, emerged on vegetation; T_b warmer than T_a and not different from pregnant females	Hare (2007)
W. chrysosiretica	Mana Island, Wellington	41° 40′	N (b)	Nov	*Mixed*	*12.5 ± 0.7 (10.5–14.0)*	*6*	*By night, emerged on vegetation*	Hare (2007)
W. maculata	Stephens I, Marlborough Sounds	40° 42′	N (b)	Nov	ND	ND (15.0 – 33.0)	14	By day, some basking, some under sheet-metal roof	Werner and Whitaker (1978)
W. ‘Otago large’	Macraes Flat, Otago	45° 28′	N (b)	Sept–Nov	PF	24.1 ± 0.5 (~19–29)	29	By day, under rocks; T_b warmer than for males	Rock et al. (2002)
W. ‘Otago large’	Macraes Flat, Otago	45° 28′	N (b)	Sept–Nov	NPF	20.2 ± 1.3 (~10–28)	23	By day, under rocks; T_b not different from other repro. groups	Rock et al. (2002)
W. ‘Otago large’	Macraes Flat, Otago	45° 28′	N (b)	Sept–Nov	M	22.0 ± 0.8 (~9–27)	50	By day, under rocks; T_b cooler than for pregnant females	Rock et al. (2002)

W. ‘Otago large’	Macraes Flat, Otago	45° 28′	N (b)	Dec–Feb	PF	19.4 ± 0.7 (~9–29)	79	By day, under rocks; T_b not different from other repro. groups	Rock et al. (2002)
W. ‘Otago large’	Macraes Flat, Otago	45° 28′	N (b)	Dec–Feb	NPF	20.1 ± 0.7 (~11–29)	62	By day, under rocks; T_b not different from other repro. groups	Rock et al. (2002)
W. ‘Otago large’	Macraes Flat, Otago	45° 28′	N (b)	Dec–Feb	M	19.1 ± 0.5 (~11–29)	88	By day, under rocks; T_b not different from other repro. groups	Rock et al. (2002)
W. ‘Otago large’	Macraes Flat, Otago	45° 28′	N (b)	*Dec*	*Mixed*	*10.1 ± 0.3 (7–13)*	22	*By night, but only two were emerged*	Rock et al. (2002)
Skinks									
Oligosoma aeneum	Mangere Mountain and One Tree Hill, Auckland	36° 54–36° 57′	Diurnal, secretive	Sept–Nov	ND	18.1 ± 0.1 (~14–24)	41	By day, under rocks; T_b higher than under-rock temperature	Porter (1987)
Oligosoma aeneum	Mangere Mountain and One Tree Hill, Auckland	36° 54–36° 57′	Diurnal, secretive	Dec–Feb	ND	22.0 ± 0.1 (17–25)	41	By day, under rocks; T_b higher than under-rock temperature	Porter (1987)
O. lineoocellatum	Motunau I, Kaitorete Spit and outdoor enclosure, Canterbury	43° 04′–43° 49′	D	Oct–Dec	ND	ND (~10–33.9)	~163	By day; including basking individuals (possibly with resampling in enclosure)	Morris (1971)
O. maccanni	Macraes Flat, Otago	45° 28′	D	Oct–Feb	PF	22.9 ± 0.6 (7.2–32.7)	117	By day; including basking and non-basking days; T_b not different from nonpregnant females and males	Hare et al. (2009)
O. maccanni	Macraes Flat, Otago	45° 28′	D	Oct–Feb	NPF & M	21.5 ± 0.7 (7.1–31.7)	89	By day; including basking and non-basking days; T_b not different from pregnant females	Hare et al. (2009)

(continued)

Table 9.2 (continued)

Species	Location and region	Latitude (°S)	Daily foraging period	Month/ season	Repro. group	T_b (°C)	*N*	Time of day and comments on location/ activity	Source
[a]*Oligosoma* spp. (probably *O. maccanni*/ *polychroma*)	Motunau I and Kaitorete Spit, Canterbury	43° 04′–43° 49′	D	Varied, including Nov	ND	25.2 ± ND (13.6–32.9)	35	By day, most individuals active	Morris (1974, 1981)
O. ornatum	Mangere Mountain and One Tree Hill, Auckland	36° 54–36° 57′	C	Sept–Nov	ND	17.0 ± 0.1 (~14.0–20.0)	29	By day, under rocks; T_b higher than under-rock temperature	Porter (1987)
O. ornatum	Mangere Mountain and One Tree Hill, Auckland	36° 54–36° 57′	C	Dec–Feb	ND	21.7 ± 0.0 (~20.0–25.0)	33	By day, under rocks; T_b higher than under-rock temperature	Porter (1987)

Daytime values are in roman type; nighttime values are in *italics*. Daily foraging periods are from source cited or Jewell (2011)

D = forages diurnally; N (b) = forages nocturnally, but also basks; C = forages dawn and dusk/crepuscular. Repro. group = reproductive group (*PF* pregnant female, *NPF* non-pregnant female, *F* female, reproductive condition unknown, *M* male). *ND* no data

[a] Assumptions have been made about probable species identity where taxonomic changes have occurred

9.3 Effects of Temperature on Performance of, and Enzyme Activity in, Isolated Tissues

Activity and locomotion of lizards, which are highly dependent on T_b, rely on muscle activity and physiological measures such as ventilatory rate, blood oxygen affinity and activity of aerobic and anaerobic enzymes (Hochachka and Somero 2002; Bennett 1982, 1983). The modest information available confirms that, unsurprisingly, temperature (within biological limits) positively influences muscle and enzyme activity. For example, the isometric twitch tension (contractility) of isolated, pubioschiotibialis muscle of *Oligosoma* spp. ([as. *Leiolopisma zelandica*], probably *O. maccanni*/*O. polychroma*) has the greatest muscle tension (at least 70 %) between 5 and 40 °C (approximately the thermal tolerance limits of the species), falling to 51 % at 0 °C with marked temperature sensitivity below 5 °C (Fig. 9.2a; Morris 1982). Muscle tension also falls above 40 °C but is still 33 % of the maximum value at 45 °C, even though individuals would be dead at this temperature (Morris 1982). Unsurprisingly, the oxygen affinity of blood haemoglobin decreases after exercise, with a corresponding shift of the equilibrium curve to the right in those species tested (*O. smithi* and *Oligosoma* spp. [as *Leiolopisma zealandica*], probably *O. polychroma*/*O. zelandicum*; Ashby 1985). Of interest, the haemoglobin concentrations, oxygen capacities, packed cell volumes and erythrocyte counts of these skinks are among the lowest reported for reptiles (Ashby 1985). Additionally, haematology does not differ between warm-acclimated and cold-acclimated *O. smithi*, and despite oxygen affinity being similar among seasons, it appears to reduce with time spent in captivity (Ashby 1985). Time spent in captivity also reduces maximal sprint speed of lizards (Hare et al. 2012) and is probably related to a physiological change such as reduced oxygen affinity of blood (Ashby 1985), to being ‘overweight’ (Connolly and Cree 2008) and/or to changes in muscles, such as atrophy.

Lactate dehydrogenase (LDH), a key metabolic enzyme involved in the glycolytic pathway, is correlated with endurance (Hochachka and Somero 2002). The specific activity and thermal sensitivity of LDH from tail muscle tissue among six New Zealand lizard species increased between 5 and 35 °C (Hare et al. 2005). However, across the temperatures, LDH activity showed no consistent pattern with activity period or lineage; instead, patterns appeared to be species specific (e.g. see Fig. 9.2b for comparison between a nocturnally foraging gecko and a diurnal, heliothermic skink; Hare et al. 2005). Potentially, LDH has adapted to function over a broad range of daily temperatures rather than specifically at the low temperatures experienced at night. In *Oligosoma* spp. ([as *L. zelandica*], probably O. *maccanni*/*O. polychroma*), glycolytic enzymatic activity of skeletal muscle is lower during winter at 5 °C, but muscle glycogen stores are preserved (Pollock and MacAvoy 1978). Conversely, oxidative enzymatic activity is less uniformly reduced in the skeletal muscles of *Woodworthia* ‘Central Otago’ ([as *H. pacificus*]) and the *Oligosoma* spp. (Pollock and MacAvoy 1978). It is worth noting that, although New Zealand lizards become torpid and remain in deep retreats during

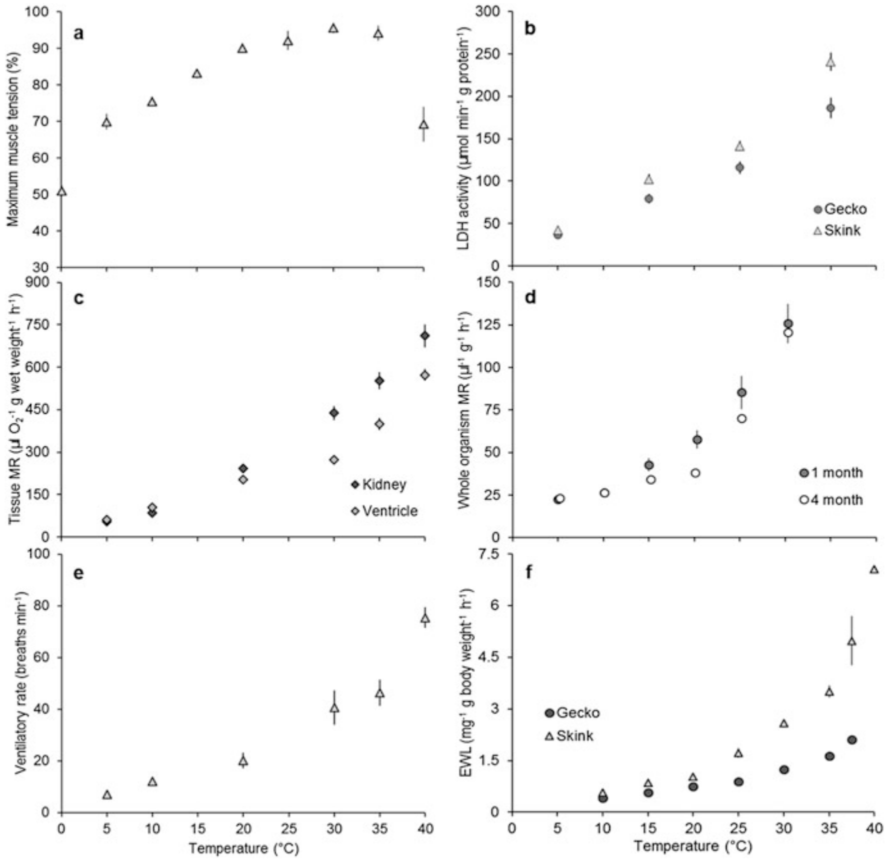


Fig. 9.2 The influence of body or tissue temperature on some physiological measures of skinks and geckos from New Zealand, including: (**a**) Mean isometric twitch tension (±1 SE) of excised puboischiotibialis muscle of skinks (*Oligosoma* spp. [as '*Leiolopisma zelandica*']; $n = 12$). Data reprinted with permission from Morris (1982), Copyright ©Elsevier 1982 [Reprinted from Comparative Biochemistry and Physiology, Part A, 71(4), Morris, Effect of temperature on muscle contractility of the eurythermic lizard *Leiolopisma zelandica*, Fig. 2, pp. 636., Copyright (1982), with permission from Elsevier.]. (**b**) Specific activity of the enzyme lactate dehydrogenase (LDH; ±1 SE) from tail muscle of geckos (*Woodworthia maculata*; $n = 31$) and skinks (*O. polychroma*; $n = 22 - 24$). Data reprinted with permission from Hare et al. (2005), Copyright ©Elsevier 2005 [Reprinted from Comparative Biochemistry and Physiology, Part B, 142(4), Hare et al., Total lactate dehydrogenase activity of tail muscle is not cold adapted in nocturnal lizards from cool-temperate habitats, Fig. 1, pp. 441., Copyright (2005), with permission from Elsevier.]. (**c**) Mean metabolic rate (MR; ±1 SE), measured as oxygen consumption of isolated kidney and ventricle tissue, from skinks (*Oligosoma* spp. [as '*L. zelandica*']; $n \leq 10$). Data reprinted with permission from Morris (1980), Copyright ©Elsevier 1980 [Reprinted from Comparative Biochemistry and Physiology, Part A, 66, Effects of temperature on metabolic rates of isolated tissues from the eurythermic lizard *Leiolopisma zelandica*, Fig. 1d and 1 h, pp. 128., Copyright (1980), with permission from Elsevier.]. (**d**) Mean whole-animal metabolic rate (MR; ±1 SE) measured as rate of oxygen consumption of adult male geckos (*Woodworthia* cf. *brunnea* [as '*Hoplodactylus maculatus*' Banks Peninsula]; $n = 10 - 13$) after acclimation to cool temperatures (5 °C) for 1 or 4 months. Reprinted with permission from Tocher and Davison (1996), Copyright ©John Wiley & Sons, Inc 1996 [Reprinted from Tocher and Davison, Differential thermal acclimation of metabolic rate in two populations of the New Zealand common gecko *Hoplodactylus maculatus*

very cold periods, many do not completely cease activity and may emerge during winter; for example, *O. grande* and *O. otagense* bask on sunny winter days on rocks surrounded by snow (Tocher 2003).

9.4 Effects of Temperature and Other Factors on Rates of Metabolism and Ventilation

Measures of metabolism can help to identify potential energetic constraints on individual organisms and may provide mechanistic explanations for large-scale ecological and evolutionary patterns (Bennett and Dawson 1976). Metabolic rate (MR) is the rate at which energy is used and, in whole organisms, is often inferred from the rate of oxygen consumption (ml O_2 g^{-1} h^{-1}) and/or production of carbon dioxide (ml CO_2 g^{-1} h^{-1}). Unsurprisingly, all measures of MR in New Zealand lizards, whether on whole animals or muscles, are influenced by temperature (e.g. Morris 1980, 1981, 1984) and follow the broad overall pattern of increasing with temperature within biological limits. The MR of isolated body tissues (μL O_2 g wet weight^{-1} h^{-1}) was measured at 5–40 °C in *Oligosoma* spp. ([as *L. zelandica*], probably *O. maccanni*/*O. polychroma*); the most metabolically active tissues were the intestine, ventricular muscle, brain and kidney (Fig. 9.2c; representative tissue from kidney shown) followed by testis and liver (Morris 1980), whereas skeletal muscle and fat bodies had much lower MR. Similarly, MR increased linearly with temperature for all aforementioned tissues except skeletal and ventricular muscle (Fig. 9.2c; representative tissue from ventricular muscle shown), in which MR was relatively independent of temperature between 20 and 30 °C (Morris 1980).

As many factors can influence whole-organism MR (e.g. reproductive condition, aestivation, season, sloughing, thermal acclimation, time of day, latitude and stress; Bennett and Dawson 1976), investigators aim to eliminate as many variables as possible when examining the factors of interest. For example, once appropriate

◄

Fig. 9.2 (continued) (Reptilia: Gekkonidae), 275:8–14, Fig. 1b. Copyright ©1996 by The Journal of Experimental Biology. Reprinted by permission of John Wiley & Sons, Inc.]. (**e**) Mean ventilatory rate of skinks (*Oligosoma* spp. [as '*L. nigriplantare*']; $n = 20$ (10 for 40 °C). Data reprinted with permission from Morris (1984), Copyright ©Elsevier 1984 [Reprinted from Comparative Biochemistry and Physiology, Part A, 77(2), Morris, Effect of temperature on the ventilatory responses of the eurythermic lizard *Leiolopisma nigriplantare*, Fig. 2, pp. 375. Copyright (1984), with permission from Elsevier.]. (**f**) Mean rate of evaporative water loss (EWL; ±SE) of adult geckos (*Woodworthia* 'Central Otago' [as '*Hoplodactylus pacificus*']; $n = 6 - 12$) and skinks (*Oligosoma* spp. [as '*L. zelandica*']; $n = 5 - 11$) under dry conditions. Data reprinted with permission from dissertation author E. S. MacAvoy (née Cook) 1969 [Reprinted with permission from E. S. MacAvoy (née Cook) who allowed use of unpublished data from her BSc Honours dissertation: Cook, E. S. 1969. A comparison of rates of water loss by evaporation, rates of carbon dioxide expiration, and ventilation rates in two New Zealand lizards, *Leiolopisma zelandica* (Gray) and *Hoplodactylus pacificus* (Gray). University of Otago. Figs. 4 and 5.]

variables are controlled for, MR is constant among populations of the same species where populations are within latitudinal, elevational and seasonal bounds (e.g. *W. maculata;* Hare et al. 2006). Similarly, for lizards in nonreproductive condition, the sex of an individual has no effect on MR (*O. aeneum*, *O. zelandicum*, *O. polychroma*, *W. maculata* and *Toropuku stephensi;* Hare et al. 2006; Hare et al. 2010). However, corticosterone-treated *W.* 'Otago large' consume oxygen at a rate approximately 50 % higher than placebo-treated geckos (Preest and Cree 2008). Similarly, exposure to novel environments results in increased MR for *N. manukanus,* indicating that habituation to experimental conditions is required prior to measuring MR (Hare et al. 2004, 2007). Control of such variables allows robust data to be collected for more involved questions, including effects of time of day (Hare et al. 2006), acclimation temperature (Tocher and Davison 1996), broad temperature ranges (Morris 1981), season and activity period (Hare et al. 2010). Here, we provide a broad summary of responses to several factors (see below and Table 9.3).

Many biochemical, physiological and behavioural parameters exhibited by animals have daily fluctuations. Daily fluctuations in MR may, among other functions, serve as an energy-conserving mechanism during the inactive part of the day (reviewed by Bennett and Dawson 1976). A study examining effects of time of day on MR in eight lizard species at low T_b (13 °C) concluded that three daily patterns of MR are present: 24 h rhythms, 12 h rhythms or no discernible daily rhythm (Table 9.3; Hare et al. 2006). Unexpectedly, the time of peak MR did not always coincide with the species' purported activity period for foraging (Hare et al. 2006). This outcome implies that MR may not be linked to activity period/ light levels and instead may allow emergence at any time that conditions permit; alternatively or additionally, activity periods for foraging may not be accurately known or classified.

The effects of a broad range of temperatures on MR of New Zealand lizards have been explored for five species (Tocher and Davison 1996; Morris 1981; Evetts and Grimmond 1982). In general, these species follow the expected patterns seen in reptiles overseas; that is, an increase in MR with increased temperature (e.g. Bennett and Dawson 1976). However, plateaus in MR often occur, but the range of temperatures over which these occur appears to be species and/or context specific. For example, in a skink and gecko, rates of carbon dioxide production are relatively independent of temperature between test T_b of 10–20 °C (Cook 1969), but in other species rates of oxygen consumption are independent of temperature between T_b of 20–30 °C (Grimmond and Evetts 1980; Table 9.3). Furthermore, marked changes in MR (and whether temperature independence exists) can occur when animals are exposed to different acclimation temperatures (Tocher and Davison 1996). For example, *W.* cf. *brunnea* and *W.* 'Southern Alps' ([as *H. maculatus*] in Tocher and Davison 1996) both show a significant reduction in MR at six experimental temperatures (between 5 and 30 °C) after long-term (4 months) acclimation to low temperature (4 °C) compared with only 1 month acclimation (Fig. 9.2d; Tocher and Davison 1996). Interestingly, *W.* cf. *brunnea* acclimated to 25 °C for 1 month, when compared to those acclimated to 5 °C for

Table 9.3 Variables in addition to body temperature (T_b) that affect metabolic rate (MR), measured as rate of oxygen consumption (mL $O_2\,g^{-1}\,h^{-1}$) or [a] carbon dioxide production (mL $CO_2\,g^{-1}\,h^{-1}$), in NZ lizards

Variable of interest	Species	Experimental variables	Outcome(s)	*N*	Test T_b	Source
Acclimation duration	[a]*Woodworthia* cf. *brunnea*	1 vs. 4 months at 5 °C	• A longer acclimation time resulted in lower MR at test T_b ranging from 15 to 25 °C • No difference between acclimation groups for MR at other test T_b	10–13 each treatment	5–30 °C (in 5 °C increments)	Tocher and Davison (1996)
Acclimation duration	[a]*Woodworthia* 'Southern Alps'	1 vs. 4 months at 5 °C	• A longer acclimation time resulted in lower MR at test T_b ranging from 5 to 20 °C • No difference in MR with acclimation duration at other test T_b • Temperature independence at 15–20 °C for geckos acclimated for 4 months	10–13 each treatment	5–30 °C (in 5 °C increments)	Tocher and Davison (1996)
Acclimation temperature	*Oligosoma* spp. (probably *O. maccanni*, potentially *O. polychroma* and *O. inconspicuum*)	Cold (4 °C) vs. warm (25 °C) acclimation	• Cold-acclimated skinks have higher MR than warm-acclimated skinks at test T_b • Difference in MR between acclimation groups greatest at T_b of 25 °C	5 each treatment	5 °C and 25 °C	Grimmond and Evetts (1980)
Acclimation temperature	[a]*Woodworthia* cf. *brunnea*	Cold (5 °C) vs. warm (25 °C)	• Cold-acclimated geckos have reduced MR at test T_b of 5 °C and 10 °C • No difference in MR between acclimation groups at test $T_b \geq 15$ °C	10–13 each treatment	5–30 °C (in 5 °C increments)	Tocher and Davison (1996)

(continued)

Table 9.3 (continued)

Variable of interest	Species	Experimental variables	Outcome(s)	*N*	Test T_b	Source
			• Temperature independence at 5–10 °C for warm-acclimated geckos			
Acclimation temperature	[a]*Woodworthia* ‘Otago large’	Cool (12–16 °C) vs. warm (26–28 °C)	• No difference in MR between acclimation groups at either test T_b	10 animals	18 °C and 28 °C	Morris (1965)
Acclimation temperature	[a]*Woodworthia* ‘Otago large’	Cold (4 °C) vs. warm (25 °C)	• Cold-acclimated geckos have lower MR than warm-acclimated geckos at test T_b of 5 °C • No difference in MR between acclimation groups at test T_b of 25 °C	5 each treatment	5 °C and 25 °C	Grimmond and Evetts (1980)
Acclimation temperature	[a]*Woodworthia* ‘Southern Alps’	Cold (5 °C) vs. warm (25 °C)	• Cold-acclimated geckos have higher MR than warm-acclimated geckos at test T_b $\geq$10 °C • Cold-acclimated geckos have lower MR than warm-acclimated geckos at test T_b of 5 °C • Temperature independence at 5–10 °C for warm-acclimated geckos	10–13 each treatment	5–30 °C (5 °C increments)	Tocher and Davison (1996)
Corticosterone treatment	*Woodworthia* ‘Otago large’	Corticosterone- vs. placebo-treated (all underwent surgery)	• Corticosterone-treated geckos had MR approximately 50 % higher than placebo geckos at each test T_b	9 each treatment	10 °C and 25 °C	Preest and Cree (2008)

Daily activity period	Nocturnally foraging: *Woodworthia maculata*, *W. chrysosiretica*, *Toropuku stephensi*, *Oligosoma macgregori* Diurnally foraging: *O. polychroma*, *O. zelandicum*, *Naultinus manukanus*; *O. aeneum*	Nocturnally foraging vs. diurnally foraging	• MR significantly higher in nocturnally foraging lizards than in diurnally foraging lizards at test T_b of 13 °C • MR similar between foraging groups at test T_b of 26 °C. • Species-specific differences and mass-scaling explain differing patterns of thermal sensitivity among species	14–69 per treatment	13 °C and 26 °C	Hare et al. (2010)
Daily activity period	(See row above)	Time of day that maximum MR observed in nocturnally foraging vs. diurnally foraging species	• *N. manukanus* (diurnal) maximum MR around midday • *W. chrysosireticus* and *O. macgregori* (nocturnal) maximum MR in early scotophase • *O. aeneum* (crepuscular) maximum MR at dawn and dusk • *O. polychroma* and *O. zelandicum* (diurnal) maximum MR during late scotophase • *W. maculata* (nocturnal) no discernible peak in MR • *T. stephensi* (nocturnal) maximum MR during early photophase	7–11 per species	13 °C	Hare et al. (2006)
Environmental moisture	*Oligosoma* spp. (probably including *O. maccanni*/*O. polychroma*)	Wet vs. dry	• [a]MR greater in skinks held under dry than humid conditions when test $T_b \geq 20$ °C	5–16 each treatment	10–35 °C (in 5 °C increments)	Cook (1969)

(continued)

Table 9.3 (continued)

Variable of interest	Species	Experimental variables	Outcome(s)	*N*	Test T_b	Source
			• Temperature independence in [a]MR when test $T_b < 20$ °C for skinks held under dry or humid conditions			
Environmental moisture	[a]*Woodworthia* 'Central Otago'	Wet vs. dry	• [a]MR lower from geckos held under dry vs. humid conditions at all test T_b • Temperature independence in [a]MR when test $T_b < 20$ °C for geckos held under dry or humid conditions	4–14 each treatment	10–35 °C (in 5 °C increments)	Cook (1969)
Habituation to metabolic chambers	*Naultinus manukanus*	Effect of trial order (habituation) on MR	• MR in trial 1 significantly higher than subsequent trials	22 animals	24 °C	Hare et al. (2004)
No treatment	*Oligosoma* spp. (probably *O. maccanni*, potentially *O. polychroma* and *O. inconspicuum*)	No treatment	• Temperature independence at test T_b of 20–30 °C	5 each test T_b	10–30 °C	Grimmond and Evetts (1980)
No treatment	[a]*Woodworthia* 'Otago large'	No treatment	• Temperature independence at test T_b of 20–30 °C	5 each test T_b	10–30 °C	Grimmond and Evetts (1980)
Season	*Oligosoma* spp. (probably *O. maccanni*, maybe including *O. polychroma*)	Winter (July–August) vs. summer (January)	• No seasonal difference in MR at any test T_b	15–52 per treatment	−5–35 °C (in 5 °C increments)	Morris (1981)
Season	*Woodworthia maculata*	Spring (November) vs. summer (January–April)	• No seasonal difference in MR	7 animals	13 °C	Hare et al. (2006)

[a] Assumptions have been made about probable species identity where taxonomic changes have occurred. Temperature independence is indicated where MR plateaus between test temperatures (i.e., where Q_{10} is close to 1)

1 month, had much higher MR at low T_b (and no difference when T_b was higher than 15 °C). Conversely, *W.* 'Southern Alps' had greater MR at all temperatures when acclimated to 5 °C than when acclimated to 25 °C (Tocher and Davison 1996). These two species had differing MR at each T_b (Tocher and Davison 1996), but whether these differences are species specific or related to long-term physiological changes resulting from living in different environments is unclear.

A numerical way of expressing the degree of thermal sensitivity is to calculate the temperature coefficient (Q_{10}; see Table 9.1 for details). The Q_{10} values for MR in New Zealand lizards appear to be lower than for comparable species overseas over the same temperature ranges, but data are patchy and difficult to compare given the differences in variables tested (Hare et al. 2010). In general, New Zealand's nocturnally foraging lizards, and *N. manukanus* (secondarily diurnal), have higher MR at low temperatures (resulting in lower Q_{10} values) than in diurnal skinks (Hare et al. 2010); thus, metabolism of nocturnally foraging lizards is less influenced by changes in T_a.

In contrast to studies overseas, and despite the obvious changes in MR after exposure to different acclimation temperatures in the laboratory, no influence of season on MR in New Zealand lizards has been found. For example, at a range of T_b, MR in summer (January) was similar to that in winter (July–August) for *Oligosoma* spp. ([as *L. zelandica*] probably *O. maccanni*/*O. polychroma*; Morris 1981), and MR in spring (November) was similar to that in summer (January–April) for *W. maculata* at T_b of 13 °C (Hare et al. 2006). These patterns are consistent with the (at least sporadic) field activity that continues throughout winter in many New Zealand lizards. Potentially these species compensate for seasonal differences in T_a in the field by thermoregulating more effectively and therefore avoiding exposure to the potentially more extreme (and often more stable) temperatures used in laboratory acclimation trials. We also note that oxygen affinity of haemoglobin in *O. smithi* and *Oligosoma* spp. is similar between seasons (Ashby 1985).

In some *Oligosoma* spp. ([as *L. nigriplantare*], probably *O. maccanni*/*O. polychroma*), mean ventilatory rates are highly temperature dependent, increasing from 7.4 to 78 breaths min^{-1} between 5 and 40 °C (i.e. increasing up till the lethal temperature; Fig. 9.2e; Morris 1984). In comparison to most overseas lizards, ventilatory rate does not drop abruptly at temperatures of 10–15 °C, but only below 5 °C; ventilatory rate was sporadic, but still observable, at temperatures as low as −1.3 °C (Morris 1984). A similar pattern of increasing ventilation rate at T_b of 20–40 °C is seen in other *Oligosoma* spp. (Cook 1969). Ventilatory rate of a gecko ([as *H. pacificus*], probably *W.* 'Central Otago') increases between 20 and 30 °C and drops between 30 and 35 °C (Cook 1969). Additionally, in other *Woodworthia* spp. ([as *H. pacificus*], probably *W.* cf. *brunnea*), peak breathing occurs at sunset, regardless of activity (McIvor 1973).

9.5 Locomotor Efficiency in Nocturnal Foragers

Studies of the energetic cost of animal locomotion have two generalisations: (1) the specific cost of locomotion (C_{min}; See Table 9.1) decreases with increasing body mass, and (2) C_{min} is dependent on the mode of locomotion used by an animal (see review in Alexander 2005). C_{min} can be calculated by measuring MR during progressively faster speeds during steady exercise on a treadmill at a set T_b; four New Zealand lizards (two skinks, two geckos) have been tested. Comparisons among these species, and with other lizards worldwide, indicate that: (1) in general, nocturnally foraging lizards have a lower C_{min} than diurnal lizards and (2) similar to nocturnal lizards, diurnal lizards that experience low temperatures during their active period also have a low C_{min} (Hare et al. 2007). The low C_{min} of lizards from cool-temperate locales may be a mechanism that facilitated range extension of lizards (skinks and geckos) into the cool-temperate regions of New Zealand. A low C_{min} enables species active at low temperatures to reach speeds normally only achievable at much higher temperatures. However, a low C_{min} does not fully compensate for the thermal handicap of activity at low temperatures.

9.6 Effects of Temperature and Other Factors on Evaporative Water Loss

Rates of evaporative water loss (EWL; combining respiratory and cutaneous loss; mg H_2O^{-1} g body mass^{-1} h^{-1}) are important to consider when predicting habitat use by lizards (Neilson 2002; Cox and Cox 2015). Unsurprisingly, EWL increases with temperature. For example, under dry test conditions, EWL of *Oligosoma* skinks and a gecko ([as *H. pacificus*], probably *W.* 'Central Otago') generally increases with increasing temperature (Cook 1969). However, under dry test conditions, the gecko has a plateau in EWL at intermediate temperatures (Fig. 9.2f). The skinks have higher EWL under dry than humid conditions at all T_b; but the gecko has higher EWL under dry conditions, though only at intermediate temperatures (Cook 1969).

In general, lizards from moist environments tend to have higher EWL than those from drier environments (Cox and Cox 2015), and larger individuals have lower EWL than smaller individuals on a mass-specific basis (Neilson 2002). Neilson (2002) investigated EWL to aid conservation management of *O. striatum* and *O. homalonotum*, two New Zealand skinks anecdotally associated with moist environments. The lizards were first held under humid (95–100 % relative humidity; rh) conditions for 28 days, then acclimated to dry (48–65 % rh) conditions for 28 days; *O. striatum* showed no difference in EWL between acclimation treatments, but *O. homalonotum* had higher rates of EWL when acclimated to dry conditions (Neilson 2002). However, under dry conditions both species were often seen submerged in their water dish (Neilson 2002), which may have influenced the outcomes. When held under humid conditions and compared with two less-threatened species from semiarid environments (*O. infrapunctatum* and *O. fallai*), both *O. striatum* and *O. homalonotum* had higher rates of mass-specific EWL (by 34 %), indicating they are adapted to inhabit moist environments (Neilson 2002).

Cutaneous water loss (CWL) has been determined for two nocturnally foraging and three diurnal skinks (Cree and Daugherty 1991). The CWL in skinks acclimated to humid conditions (95–100 % rh) is higher in nocturnally foraging species (3.5 mg g^{-1} h^{-1}) compared with diurnal skinks (1.7 mg g^{-1} h^{-1}). For three species also tested after 30 days acclimation to drier conditions (50–65 % rh; *O. alani*, *O. infrapunctatum* and *O. lineoocellatum*), only *O. lineoocellatum* has a significantly different (lower) CWL. Rates of CWL for diurnal species are comparable to lizard species from overseas, but it appears that nocturnal lizards in New Zealand have high rates of cutaneous water loss that, at least in *O. alani*, may be a fixed trait (Cree and Daugherty 1991).

9.7 Physiological Comparisons with Lizards Elsewhere and with Tuatara, and Some Possible Implications of Climate Change

Our review reveals a number of physiological characteristics that have plausibly evolved as a response to occupying a relatively cool climate. For example, when compared with lizards from warmer climates elsewhere, New Zealand lizards (especially nocturnally foraging geckos) have low field T_b when emerged, low CT_{min}, low T_{sel} and 'left-shifted' thermal performance curves for sprint speed (e.g. Huey 1982; Clusella-Trullas et al. 2011; Huey et al. 2012 for overseas species). The plateau for peak speed (i.e. optimal temperature range, a measure of performance breadth) is also relatively large (Gaby et al. 2011). Among lizards globally, CT_{min} decreases with latitude more markedly than does CT_{max} (Clusella-Trullas et al. 2011; Huey et al. 2012); the low CT_{min} values for lizards from southern New Zealand are consistent with high latitudes. Parallels are also apparent in the way that experimental temperatures affect MR and EWL. In general, New Zealand's lizards show the expected pattern of MR increasing with increasing T_b; additionally, MR at a given temperature is within the range seen for species of similar body size overseas (Hare et al. 2010), and EWL follows consistent patterns.

Some of the same physiological characteristics as in New Zealand lizards have been documented in tuatara (*S. punctatus*), another New Zealand reptile that forages nocturnally and basks. For example, values for field T_b, CT_{min}, T_{sel} and upper lethal temperatures are similar to those in New Zealand geckos that forage nocturnally (Besson and Cree 2011; Cree 2014). Similarly, MR increases in tuatara between 5 and 30 °C, with a region of thermal insensitivity between 12 and 20 °C in some studies (see Cree 2014 for review). Rates of EWL in tuatara are also temperature sensitive (Hill 1982) and similar to those in New Zealand lizards that forage nocturnally (Cree and Daugherty 1991). As tuatara and lizards are only distantly related (their respective orders, Rhynchocephalia and Squamata, diverged ~250 million years ago), these similarities (along with their 'slow' life histories; Cree and Hare 2016) suggest common adaptations to New Zealand climates.

The implications of global climate change for lizards are receiving increasing attention from ecophysiologists. If a high-carbon economy prevails, New Zealand's annual mean T_a is predicted to be 2.6 °C higher by 2080–2099 than during 1980–1999 (Reisinger et al. 2010). A crude way of estimating a species' tolerance for such an increase is to calculate the 'thermal safety margin' or TSM (see Table 9.1 for calculation; Clusella-Trullas et al. 2011; Hoffmann et al. 2013). Global analyses suggest that tropical or mid-latitude lizards have the lowest TSMs, meaning they already operate close to their upper thermal limits (Clusella-Trullas et al. 2011; Huey et al. 2012; Hoffmann et al. 2013). We calculated the TSMs for *O. maccanni* and *W.* 'Otago large' at Macraes Flat, taking the cautious approach of using the daytime T_{sel} for the adult group with the lowest known value. The results indicate that non-pregnant *O. maccanni* ($\sim 26 - 13.4 = \sim 12.6$ °C) and male *W.* 'Otago large' ($\sim 23 - 13.4 = \sim 9.6$ °C) appear, like other high-latitude ectotherms, to have relatively large TSMs. Put another way, lizards in these populations, especially pregnant females, currently experience such low exposure to T_{sel} at Macraes Flat (Rock et al. 2002; Hare et al. 2009) that they may benefit from climate warming in some life-history respects (Cree and Hare 2016). However, possible changes in cloud cover (for which high-resolution dynamics of current conditions are only just available; Wilson and Jetz 2016) could alter the relationship between T_a and T_b, leading to uncertain changes in T_b, and there is potential for so many non-thermal effects that overall outcomes of climate change remain speculative.

9.8 Conclusions and Recommendations for Future Studies

New Zealand lizards have typically shaped (asymmetrical) performance curves for sprint speed relative to T_b, but the curves are 'left shifted' compared with many overseas species. In particular, CT_{min} and T_{SEL} are relatively low, as expected for high-latitude species with low field T_bs. Some thermal parameters are particularly left shifted for geckos generally, including for nocturnal foragers that also cryptically bask; however, evidence for skinks is limited. At Macraes Flat, both the diurnal skink *O. maccanni* and the nocturnally foraging gecko *W.* 'Otago large' (especially pregnant females) reach T_{SEL} only infrequently. Even for non-pregnant females or males, their TSM is relatively large (typical for high-latitude lizards globally), suggesting that these species may benefit from warmer temperatures with climate change.

As expected, within biological limits, an increase in T_b results in increasing rates of various physiological measures, including whole-organism MR, MR of tissues, ventilatory rate and rate of EWL. Additionally, as expected these rates are influenced by many factors, including pregnancy status, acclimation to various environments (thermal or rh) and changes in hormone levels. However, in contrast to studies overseas, season appears not to influence MR of New Zealand lizards. Also of interest is the repeating theme of a temperature range over which many physiological measures are relatively temperature independent. This region of independence generally occurs somewhere between 15 and 30 °C, although, for MR in particular, some species show it at lower temperatures (Table 9.3). For example, temperature independence is reported in: (1) tissues involved in locomotion (ventricular and skeletal muscle), but not other isolated tissues in a skink (Morris 1980), (2) MR of some skinks and geckos (Table 9.3), (3) blood oxygen affinity of two skinks (Ashby 1985), (4) EWL in a gecko (Cook 1969) and (5) sprint speed of a skink and gecko (Fig. 9.1; Gaby et al. 2011). These temperature-independent plateaus (where Q_{10} is ~1) indicate a region of relative thermal stability, in which aspects of physiology are less influenced by changes in temperature. That is, the physiological processes are able to be maintained at what might otherwise be a rate-limiting temperature.

Similarly, nocturnally foraging New Zealand lizards, and *N. manukanus* (secondarily diurnal), have higher MR at low temperatures than diurnal species (Hare et al. 2010). This suggests that the MR of nocturnally foraging lizards is less influenced by changes in temperature, whereas MR of diurnal lizards will increase rapidly with changing temperature, as expected; that is, diurnal species have a more rapid response of MR to an increase in environmental temperature. Nocturnally foraging lizards also have a low $C_{\min}$, but surprisingly so do diurnal lizards from New Zealand; this low $C_{\min}$ *partially* offsets the thermal handicap imposed on lizards active at low temperatures. Other physiological mechanisms may also help further compensate for the thermal handicap, or lizards in New Zealand may simply be somewhat inefficient at low temperatures. The latter possibility has implications for the ability of New Zealand lizards to evade introduced mammalian predators, which are endothermic.

Although our review suggests some physiological differences between geckos and skinks, or between nocturnal and diurnal foragers, we note that it is not always possible to distinguish clearly between these alternative interpretations. This difficulty arises because of the limited range of species studied and because of limited and/or incomplete information on activity periods. Our review has also identified some other knowledge gaps, and more generally it illustrates the limited range of physiological topics explored to date for New Zealand lizards. We suggest that information on many aspects of physiology is relevant to conservation management and likely to become increasingly so in the context of climate change. To improve our understanding of evolutionary patterns in the physiology of New Zealand lizards and to better predict possible effects of climate change, we recommend the following:

1. Field ecologists should report both T_a and T_b whenever possible (noting that T_{skin} for small-bodied species can be measured non-invasively using an infrared thermometer as an alternative to cloacal T_b; Hare et al. 2007).
2. Physiological studies (spanning both field and laboratory settings) are needed on a wider range of species, topics and habitats. In particular, more information is needed on subtropical species from northern New Zealand, on lowland vs. highland species in the same latitudinal range, on high-latitude/high-elevation (alpine) species from southern New Zealand, and on nocturnal skinks and diurnal geckos.
3. To better predict possible effects of global climate change, we need to know (1) whether cloud cover will change as T_a increases, and if so how this will affect field T_b; (2) the effects of combined changes in T_b and moisture availability on physiological performance.
4. More robust behavioural data are needed on activity periods. For example, activity periods could be assessed using time series (e.g. Hare et al. 2016), and/or camera stations.

Acknowledgements We thank Ken Miller for graphical assistance; Georgia Moore and Jenny Rock for use of their photos; David Chapple, Marieke Lettink and Rod Hitchmough for taxonomic information; and David Chapple, Scott Jarvie and Mike Thompson for useful suggestions on the draft. For permission to reproduce or adapt material or information from published sources, we thank Elsevier, John Wiley and Sons (Inc.), and Springer, as well as Elizabeth MacAvoy (née Cook) for use of data from her honours dissertation and Jon Hare for re-use of published data in a different format.

References

Alexander MR (2005) Models and the scaling of energy costs for locomotion. J Exp Biol 208:1645–1652

Angilletta MJ Jr (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford

Ashby MD (1985) Factors affecting blood physiology and haemoglobin function in the New Zealand skinks, *Leiolopisma smithi* (Gray) and *Leiolopisma zelandica* (Gray). Comp Biochem Physiol 80A:31–40

Autumn K, Weinstein RB, Full RJ (1994) Low cost of locomotion increases performance at low temperature in a nocturnal lizard. Physiol Zool 67:238–262

Barry M, Shanas U, Brunton DH (2014) Year-round mixed-age shelter aggregations in Duvaucel's geckos (*Hoplodactylus duvaucelii*). Herpetologica 70:395–406

Barwick RE (1982) The growth and ecology of the gecko *Hoplodactylus duvaucelii* at The Brothers Islands. In: Newman DG (ed) New Zealand herpetology, vol 2, New Zealand Wildlife Service. Occasional Publication, Wellington, pp 377–398

Bennett AF (1982) The energetics of reptilian activity. In: Gans C, Pough FH (eds) Biology of the Reptilia—Physiology D, vol 13. Biology of the reptilia. Academic Press, London, pp 155–199

Bennett AF (1983) Ecological consequences of activity metabolism. In: Huey RB, Pianka ER, Schoener TW (eds) Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, MA, pp 11–23

Bennett AF, Dawson WR (1976) Metabolism. In: Gans C, Dawson WR (eds) Biology of the Reptilia—Physiology A, vol 5. Academic Press, London, pp 127–223

Besson AA, Cree A (2011) Integrating physiology into conservation: an approach to help guide translocations of a rare reptile in a warming environment. Anim Conserv 14:28–37

Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Clusella-Trullas S, Blackburn TM, Chown SL (2011) Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. Am Nat 177:738–751

Coddington E, Cree A (1997) Population numbers, response to weather, movements and management of the threatened New Zealand skinks *Oligosoma grande* and *O. otagense* in tussock grasslands. Pac Conserv Biol 3:379–391

Connolly JD, Cree A (2008) Risks of a late start to captive management for conservation: phenotypic differences between wild and captive individuals of a viviparous endangered skink (*Oligosoma otagense*). Biol Conserv 141:1283–1292

Cook ES (1969) A comparison of rates of water loss by evaporation, rates of carbon dioxide expiration, and ventilation rates in two New Zealand lizards, *Leiolopisma zelandica* (Gray) and *Hoplodactylus pacificus* (Gray). Unpublished BSc honours dissertation, University of Otago, Dunedin

Cox CL, Cox RM (2015) Evolutionary shifts in habitat aridity predict evaporative water loss across squamate reptiles. Evolution 69:2507–2516

Cree A (2014) Tuatara: biology and conservation of a venerable survivor. Canterbury University Press, Christchurch

Cree A, Daugherty CH (1991) High rates of cutaneous water loss in nocturnal New Zealand reptiles. Unpublished report, Wellington Conservancy, New Zealand Department of Conservation, Wellington

Cree A, Hare KM (2010) Equal thermal opportunity does not result in equal gestation length in a cool-climate skink and gecko. Herpetol Conserv Biol 5:271–282

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Cree A, Tyrrell CL, Preest MR, Thorburn D, Guillette LJ Jr (2003) Protecting embryos from stress: corticosterone effects and the corticosterone response to capture and confinement during pregnancy in a live-bearing lizard (*Hoplodactylus maculatus*). Gen Comp Endocrinol 134:316–329

Duncan P (1999) Behavioural and ecological factors affecting the trappability of two skink species in Nelson. Unpublished MSc thesis, University of Otago, Dunedin

Evetts PM, Grimmond NM (1982) The effects of temperature on oxygen consumption in *Leiolopisma nigriplantare maccanni* and *Hoplodactylus maculatus*. In: Newman DG (ed) - New Zealand herpetology, vol 2. New Zealand Wildlife Service, Wellington, pp 409–415

Gaby MJ, Besson AA, Bezzina C, Caldwell AJ, Cosgrove S, Cree A, Haresnape S, Hare KM (2011) Thermal dependence of locomotor performance in two cool-temperate lizards. J Comp Physiol A 197:869–875

Gibson R (2016) Guide to keeping New Zealand lizards in captivity. New Zealand Department of Conservation, Wellington. http://www.doc.govt.nz/Documents/about-doc/concessions-and-permits/protected-wildlife-in-captivity/best-practice-guide-keeping-lizards-in-captivity.pdf

Gibson S, Penniket S, Cree A (2015) Are viviparous lizards from cool climates ever exclusively nocturnal? Evidence for extensive basking in a New Zealand gecko. Biol J Linn Soc 115:882–895

Girling JE, Cree A (1995) Plasma corticosterone levels are not significantly related to reproductive stage in female common geckos (*Hoplodactylus maculatus*). Gen Comp Endocrinol 100:273–281

Grimmond NM, Evetts PM (1980) The effects of temperature on heat exchange and oxygen consumption in two sympatric New Zealand lizards. In: Szelényi Z, Székely M (eds) Advances in physiological sciences, contributions to thermal physiology, vol 32. Satellite symposium of the 28th International Congress of Physiological Sciences, Pecs, Hungary. Akademiai Kiado, Budapest, pp 257–259

Hare KM (2007) *Hoplodactylus chrysosireticus* (Goldstripe gecko). Body temperature. Herpetol Rev 38:456–457

Hare KM, Pledger S, Thompson MB, Miller JH, Daugherty CH (2004) Conditioning reduces metabolic rate and time to steady-state in the lizard *Naultinus manukanus* (Reptilia: Gekkonidae). Comp Biochem Physiol A 139:245–250

Hare KM, Miller JH, Clark A, Daugherty CH (2005) Total lactate dehydrogenase activity of tail muscle is not cold-adapted in nocturnal lizards from cool-temperate habitats. Comp Biochem Physiol B 142:438–444

Hare KM, Pledger S, Thompson MB, Miller JH, Daugherty CH (2006) Daily patterns of metabolic rate among New Zealand lizards (Reptilia: Lacertilia: Diplodactylidae and Scincidae). Physiol Biochem Zool 79:745–753

Hare KM, Pledger S, Thompson MB, Miller JH, Daugherty CH (2007) Low cost of locomotion in lizards that are active at low temperatures. Physiol Biochem Zool 80:46–58

Hare JR, Holmes KM, Wilson JL, Cree A (2009) Modelling exposure to selected temperature during pregnancy: the limitations of reptilian viviparity in a cool-climate environment. Biol J Linn Soc 96:541–552

Hare KM, Pledger S, Thompson MB, Miller JH, Daugherty CH (2010) Nocturnal lizards from a cool-temperate environment have high metabolic rates at low temperatures. J Comp Physiol B 180:1173–1181

Hare KM, Norbury G, Judd L, Cree A (2012) Survival of captive-bred skinks following reintroduction to the wild is not explained by variation in speed or body condition index. N Z J Zool 39:319–328

Hare KM, Chapple DG, Towns DR, van Winkel D (2016) The ecology of New Zealand's lizards. Chap. 6. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hill L (1982) Water relations and excretion of the tuatara, *Sphenodon punctatus*: an overview. In: Newman DG (ed) New Zealand herpetology, vol 2. New Zealand Wildlife Service. Occasional Publication, Wellington, pp 183–203

Hochachka PW, Somero GN (2002) Biochemical adaptation: mechanism and process in physiological evolution, vol 2. Oxford University Press, New York

Hoffmann AA, Chown SL, Clusella-Trullas S (2013) Upper thermal limits in terrestrial ectotherms: how constrained are they? Funct Ecol 27:934–949

Huey RB (1982) Temperature, physiology and ecology of reptiles. In: Gans C, Pough FH (eds) Biology of the Reptilia, vol 12. Academic, London, pp 25–92

Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos Trans R Soc B 367:1665–1679

Jewell T (1997) Low voluntary minimum temperature for activity in an alpine gecko from New Zealand. Herpetofauna 27:49–50

Jewell T (2011) A photographic guide to reptiles and amphibians of New Zealand (revised and updated). New Holland, Auckland

Kingsolver JG (2009) The well-temperatured biologist. Am Nat 174:755–768

Lettink M, Hare KM (2016) Sampling techniques for New Zealand lizards. Chap. 10. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Lutterschmidt WI, Hutchison VH (1997) The critical thermal maximum: data to support the onset of spasms as the definitive end point. Can J Zool 75:1553–1560

McIvor I (1973) Activity and daily breathing patterns of the gecko, *Hoplodactylus pacificus* Gray. Māuri Ora 1:91–94

Morris RW (1965) Temperature history and metabolic level of a New Zealand gekko. *Hoplodactylus pacificus* (Gray). Copeia 1965:248–249

Morris RW (1971) On some aspects of the biology, thermal relations and thermo-physiology of *Leiolopisma lineoocellatum*. Unpublished MSc thesis, University of Canterbury, Christchurch

Morris RW (1974) Some aspects of the thermophysiology of the skink *Leiolopisma zelandica*. Unpublished PhD thesis, University of Canterbury, Christchurch

Morris RW (1980) Effects of temperature on metabolic rates of isolated tissues from the eurythermic lizard *Leiolopisma zelandica*. Comp Biochem Physiol A 66:127–133

Morris RW (1981) Effect of a broad temperature range on the metabolic responses of the eurythermic lizard *Leiolopisma zelandica*. Comp Biochem Physiol A 70:623–626

Morris RW (1982) Effect of temperature on muscle contractility of the eurythermic lizard *Leiolopisma zelandica*. Comp Biochem Physiol A 71:635–637

Morris RW (1984) Effect of temperature on the ventilatory responses of the eurythermic lizard *Leiolopisma nigriplantare*. Comp Biochem Physiol A 77:373–376

Neilson KA (2002) Evaporative water loss as a restriction on habitat use in endangered New Zealand endemic skinks. J Herpetol 36:342–348

Nielsen SV, Bauer AM, Jackman T, Hitchmough RA, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol 59:1–22

Pollock M, MacAvoy ES (1978) Morphological and metabolic changes in muscles of hibernating lizards. Copeia 1978:412–416

Porter R (1987) An ecological comparison of two *Cyclodina* skinks (Reptilia: Lacertilia) in Auckland, New Zealand. N Z J Zool 14:493–507

Preest MR, Cree A (2008) Corticosterone treatment has subtle effects on thermoregulatory behavior and raises metabolic rate in the New Zealand common gecko, *Hoplodactylus maculatus*. Physiol Biochem Zool 81:641–650

Reisinger A, Mullan B, Manning M, Wratt D, Nottage R (2010) Global and local climate change scenarios to support adaptation in New Zealand. In: Nottage RAC, Wratt DS, Bornman JF, Jones K (eds) Climate change adaptation in New Zealand: future scenarios and some sectoral perspectives. New Zealand Climate Change Centre, Wellington, pp 26–43

Rock J, Cree A (2008) Extreme variation in body temperature in a nocturnal thigmothermic lizard. Herpetol J 18:69–76

Rock J, Andrews RM, Cree A (2000) Effects of reproductive condition, season, and site selected temperatures of a viviparous gecko. Physiol Biochem Zool 73:344–355

Rock J, Cree A, Andrews RM (2002) The effect of reproductive condition on thermoregulation in a viviparous gecko from a cool climate. J Therm Biol 27:17–27

Salmon NM (2002) Telemetric studies of the geckos *Hoplodactylus maculatus* and *Naultinus gemmeus*. Unpublished MSc thesis, University of Otago, Dunedin

Spencer NJ, Grimmond NM (1994) Influence of elevation on the thermoregulation of two sympatric lizards. N Z J Zool 21:379–385

Thierry A, Lettink M, Besson AA, Cree A (2009) Thermal properties of artificial refuges and their implications for retreat-site selection in lizards. Appl Herpetol 6:307–326

Tocher MD (1992) Paradoxical preferred body temperatures of two allopatric *Hoplodactylus maculatus* (Reptilia: Gekkonidae) populations from New Zealand. N Z Nat Sci 19:53–60

Tocher MD (1993) Critical minimum body temperatures of *Hoplodactylus maculatus* (Reptilia: Gekkonidae) from New Zealand. N Z Nat Sci 20:41–45

Tocher MD (2003) The diet of grand skinks (*Oligosoma grande*) and Otago skinks (*Oligosoma otagense*) in Otago seral grasslands. N Z J Zool 30:243–257

Tocher MD, Davison W (1996) Differential thermal acclimation of metabolic rate in two populations of the New Zealand common gecko *Hoplodactylus maculatus* (Reptilia: Gekkonidae). J Exp Biol 275:8–14

Vermunt A, Hare KM, Besson AA (2014) Unusual change in activity pattern at cool temperature in a reptile (*Sphenodon punctatus*). J Therm Biol 42:40–45

Werner YL, Whitaker AH (1978) Observations and comments on the body temperatures of some New Zealand reptiles. N Z J Zool 5:375–393

Whitaker AH (1984) *Hoplodactylus kahutarae* n. sp. (Reptilia: Gekkonidae) from the Seaward Kaikoura Range, Marlborough, New Zealand. N Z J Zool 11:259–270

Wilson AM, Jetz W (2016) Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. PLoS One (Biol) 14(3):e1002415. doi:10.1371/journal.pbio.1002415

Chapter 10
Sampling Techniques for New Zealand Lizards

Marieke Lettink and Kelly M. Hare

Abstract The New Zealand lizard fauna is represented by two lineages (Diplodactylidae geckos and Eugongylinae skinks), of which all members are small to medium sized by global standards. Methods used to sample these lizards in the field are a subset of those available worldwide, but include some notable adaptions, novel designs and techniques originally developed for the detection and monitoring of pest mammals. This chapter describes current standard field methods (systematic searching, live trapping and artificial retreats) alongside less frequently used methods (adhesive traps, detector dogs, camera stations and footprint tracking), some of which are still under development or have restricted use. We also discuss the main methods used for individual identification of New Zealand lizards: temporary marking, toe-clipping and photo-identification. When coupled with a thorough understanding of lizard behaviour and ecology, these methods collectively permit effective sampling of the majority of the New Zealand lizard fauna. Arboreal species require further attention, as does the development of accurate, fast and ethically acceptable methods for permanent marking.

Keywords Adhesive traps • Artificial retreats • Camera stations • Detector dogs • Footprint tracking • Funnel trapping • Gecko • Photo-identification • Pitfall trapping • Skink • Systematic searching • Toe-clipping

10.1 Introduction

The New Zealand lizard fauna currently consists of 104 native taxa and one introduced species (including many undescribed entities; Hitchmough et al., 2016a, b). Although species rich, taxonomic representativeness is limited to just two lineages: Diplodactylidae geckos and Eugongylinae skinks (Hitchmough

---

M. Lettink (✉)
Independent Ecologist, Fauna Finders, Christchurch, New Zealand
e-mail: marieke_kakariki@clear.net.nz

K.M. Hare
Centre for Biodiversity and Restoration Ecology, Victoria University of Wellington,
Wellington, New Zealand

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_10

et al. 2016a). By global standards, New Zealand lizards are small to medium sized (maximum snout-vent length of 160 mm in the largest species, Duvaucel's gecko, *Hoplodactylus duvaucelii*; Whitaker 1968; Cree and Hare 2016). Due to their limited taxonomic representativeness and size range, the methods used to sample these lizards in the field are a subset of those available worldwide (McDiarmid et al. 2012). However, there are some notable adaptations, novel designs and recent applications of methods originally developed for pest mammals in New Zealand.

This chapter reviews the standard field methods currently used to sample New Zealand lizards [systematic searching, live trapping and artificial retreats; reviewed by Whitaker (1994) and Lettink and Monks (2016)] and briefly explores techniques that are used infrequently (detector dogs), still under development (footprint tracking) or subject to restrictions in use (adhesive traps). For completeness, we also mention the use of camera stations, a technique that has been trialled on New Zealand lizards but is of limited use due to their small size. In addition, we detail the main methods used for individual identification of lizards. These are vital for monitoring and some long-term studies. Thus, our aims are twofold: (1) to provide a comprehensive review of sampling techniques and individual identification methods for New Zealand lizards and (2) to indicate any areas that require further research and development. In doing this, we aim to provide a resource that can be used and built on by future herpetologists.

We note that detailed prescriptions for the use of the standard field methods are available in the Herpetofauna Module of the Biodiversity Inventory and Monitoring Toolbox developed by the New Zealand Department of Conservation (DOC; Greene and McNutt 2012). Attempts to develop new sampling methods can take significant amounts of time, are not always successful or published, and may not be freely discussed due to commercial sensitivities (e.g. patents). Accordingly, this chapter includes relevant unpublished material.

10.2 Systematic Searching

Systematic searching, also known as visual encounter surveys (Guyer and Donnelly 2012), entails visual and hand searching for lizards by day and night (Whitaker 1994; Greene and McNutt 2012). Visual searching, using the naked eye and/or binoculars, targets animals that are emerged (e.g. basking, roaming or foraging). Hand searching involves locating inactive lizards within their retreat sites (e.g. under stones, logs and bark, and in tree cavities and rock crevices).

Systematic searching is primarily used to obtain information on species' presence. It is often the only method used to survey areas where herpetofaunal values are unknown. These include sites for future research, conservation (e.g. reserve designation) or development that may cause human-wildlife conflict (e.g. road corridors, mine footprints, housing developments). It may also be used for monitoring populations, typically yielding lizard counts or catch-per-unit-effort indices derived from time- or area-constrained searches (Greene and McNutt 2012; McDiarmid et al. 2012).

Advantages and disadvantages of this method are discussed in detail in Lettink and Monks (2016) and summarised in Table 10.1. Of note, it is highly effective when conducted under optimal weather conditions for emergence of the target species and is readily applied over large areas. However, it is prone to observer bias, strongly influenced by weather conditions and may be more difficult to standardise than some other field methods (Whitaker 1994). In addition, hand searching can seriously degrade lizard habitats by altering specific microhabitat features, even when care is taken to minimise disturbance (Pike et al. 2010).

Visual and hand searching may be done during the day and/or at night depending on the daily activity phase of the target species. In its most basic form, the observer (s) will slowly walk through a predefined area of interest, noting the species identity and location of lizards encountered, weather conditions and search times. Once animals are located, they may be identified on sight (using binoculars if necessary), photographed and/or captured by hand. Visual searching is most effective when done under optimal conditions for emergence of New Zealand lizards (Hare and Cree 2016). Encounter rates tend to vary with habitat structure and observer experience (Smolensky and Fitzgerald 2010).

The equipment required for visual and hand searching is minimal. Lizard locations should be recorded using a Global Positioning System (GPS). Binoculars are invaluable for searching some habitats (e.g. mobile rock screes, cliff faces and tall vegetation) and to permit identification of elusive species that do not tolerate close approach. Where close approach is not possible, a digital camera with a good zoom lens can be used to photograph animals for identification purposes. A small torch or mirror is useful to illuminate rock crevices and tree cavities. Animals in crevices can sometimes be extracted using a noose (particularly useful for skinks) or by ‘winkling’ with flexible, insulated electrical cable (Patterson 1992; Whitaker 1994). Searching at night requires a torch and/or a binocular-mounted spotlight; an experienced operator using custom-built ‘spotlighting’ gear can detect emerged geckos over distances up to 100 m, often by their eyeshine (Whitaker et al. 1999).

10.3 Live Trapping

Live trapping entails the deliberate capture of lizards in non-lethal traps that retain animals until they are released by the observer. Currently in New Zealand, live traps of any kind must be checked at least once every 24 h (a legal requirement under the Animal Welfare Act 1999). Animals constrained in traps are vulnerable to a range of potential threats, including predation, flooding, desiccation and heat stress, all of which can lead to mortality (Whitaker 1994). Live trapping is extensively used to monitor terrestrial species (particularly skinks) since it is easily repeated and standardised. In surveys, live trapping usually complements (rather than replaces) systematic searching due to the substantial time required to deploy, check and

Table 10.1 Advantages and disadvantages of current methods used for sampling lizards in New Zealand (adapted with permission from Lettink and Monks 2016)

Method	Description	Advantages	Disadvantages
Systematic searching[a]	Visual and/or hand searching. Involves looking for emerged lizards and checking potential retreat sites for inactive lizards and their sign	• Inexpensive • Often easy to repeat • Very effective in good conditions • May be only available method (e.g. if traps cannot be deployed and where sites are only visited once) • Can be conducted in poor weather conditions and used to locate nocturnal species during the day	• Observer bias • Can be labour intensive • Can be destructive to habitat and lizards if appropriate care is not taken • Not possible to identify lizard species or numbers from sign alone
Pitfall trapping[a]	Daily checks of traps recessed into the ground and covered with lids, typically 2–4 L metal tins or plastic containers baited with pear	• Easy to repeat and standardise • No observer bias • Very effective for terrestrial skinks • Proven method for long-term monitoring of terrestrial species	• Must be set up in advance • Labour intensive • Geckos can escape • Not effective for arboreal species • Not all life stages equally trappable • Predator by-catch
Funnel trapping[a]	Daily checks of baited funnel traps, e.g. Gee's minnow traps and other designs	• Easy to repeat and standardise • No observer bias • Easier to deploy than pitfall traps (no digging) • Minimal habitat disturbance	• Must be set up in advance • Labour intensive • Can be expensive (e.g. Gee's minnow traps currently cost US $33 each) • Predator by-catch (especially mice) • Effectiveness compared with pitfall traps unknown for most species
Adhesive traps	Frequent checks of glue or sticky traps placed on the ground or in trees. Attached animals must be carefully removed by applying vegetable oil	• Easy to repeat and standardise • Inexpensive and quick to deploy • Can be used to capture a wide range of species • No observer bias	• Can incur high mortality rates • Use for vertebrates is restricted in New Zealand
Artificial retreats[a]	Checks of artificial refuges or cover objects. Common designs are Onduline stacks or corrugated iron for terrestrial species and closed-cell	• Easy to repeat and standardise • Minimal habitat disturbance • Requires minimal training	• Must be set up 1–3 months in advance • Can be interfered with by wildlife, people or livestock • Permanent placement

(continued)

Table 10.1 (continued)

Method	Description	Advantages	Disadvantages
	foam covers for arboreal geckos	• No observer bias • Can be used to locate nocturnal species by day • Very effective in cool and wet areas where thermal substrates (e.g. rocks) are scarce	may alter lizard distribution and abundance, and attract predators
Camera stations	Unmanned cameras set up to detect animals on still photos or video footage	• Noninvasive • Can be used for continuous monitoring • Reduces observer field time and effort	• Viewing images is time consuming • Ineffective for small animals but this may change with future technological advances • Costs may be prohibitive if multiple camera stations are needed (e.g. monitoring arrays)
Footprint tracking	Detection of lizards by footprints left on custom-made tracking cards	• Noninvasive • Easy to repeat and standardise • Minimal habitat disturbance • No observer bias • Can be used to detect low-density populations	• Species identification may not be possible • Cannot be used to count individuals • Has not been calibrated for lizard monitoring
Detector dogs	Detection of lizards by specially trained dogs that indicate lizard presence	• Can be used to locate rare and cryptic species	• Less effective for arboreal species • Animal recovery and identification not always possible • Requires regular training and housing

[a] Prescriptions for standard methods are available from the Herpetofauna Module of the Department of Conservation's Inventory and Monitoring Toolbox (Greene and McNutt 2012). Results obtained with all methods are weather dependent to varying degrees, particularly when sampling ectothermic animals such as lizards

remove traps. Traps are particularly useful for sampling areas where lizards are difficult to detect by other means (e.g. dense grassland and fernland).

The most common types of live traps used for lizards are pitfall and funnel traps (Fig. 10.1). Pitfall traps have the longest history of use in New Zealand, particularly for monitoring terrestrial species (e.g. Whitaker 1967; Newman 1994; Hoare et al. 2007). Funnel traps have a comparatively short (<15 years) history despite extensive use elsewhere in the world (e.g. Vogt 1941; McDiarmid et al. 2012). Choice of trap type is determined by a number of factors, including their effectiveness at capturing the target species, the terrain and the cost and/or availability of traps. New Zealand lizards have also been sampled with adhesive traps and camera

Fig. 10.1 Live traps and artificial retreats used to sample New Zealand lizards (see text). Pitfall trap (**a**) with and (**b**) without lid; funnel trap (**c**) with and (**d**) without vegetation to provide shade; (**e**) adhesive trap; (**f**) artificial retreat consisting of two layers of Onduline; (**g**) mesh bin with funnel inside (photo: Les Moran); (**h**) closed-cell foam covers (Photo: Trent Bell). All other photos are by Marieke Lettink

Box 10.1: A Challenge for Future Herpetologists: Designing the Perfect Lizard Trap

To date, attempts to develop novel trap designs for New Zealand lizards have rarely been successful (i.e. produced a design that is at least as effective as existing pitfall and funnel trap designs). The ideal live trap for lizards should be inexpensive, lightweight, easily transportable (e.g. stackable or collapsible) and inconspicuous in order to avoid interference by humans and other animals, and capture and retain a wide range of arboreal and terrestrial taxa. It should also require no digging, carry no risk of overheating and exclude all mammalian predators (including mice).

traps (hereafter, camera stations), but their use is relatively uncommon. Designing a perfect live trap capable of capturing lizards in all habitats remains a challenge for future herpetologists (Box 10.1). Most important are design modifications that eliminate or significantly reduce predator by-catch and permit more effective sampling of arboreal species (particularly those living in the forest canopy) and terrestrial taxa that occupy challenging environments (e.g. alpine bluff and mobile scree habitats).

10.3.1 Pitfall Traps

A pitfall trap consists of an open-ended container buried in the ground to leave its rim flush with the surface. Animals fall into them and are unable to escape. Containers may be any shape (e.g. plastic pail, metal tin, PVC pipe, ideally with a rim that protrudes inwards; Mazerolle 2003) but must be deep enough to prevent the largest individuals from escaping (Whitaker 1994). A size of 2–4 L is adequate for most New Zealand lizard species; however, geckos and large skinks can escape from pitfall traps (Whitaker 1982). Containers must have drainage holes to prevent flooding and lids that are secured 1–2 cm above traps (Fig. 10.1). Lids provide shade for captive individuals and reduce interference by, and entry of, potential predators (mammals, reptiles, birds and invertebrates; Whitaker 1994; Greene and McNutt 2012). Unfortunately, risk of predation for any type of live trap cannot be entirely eliminated. The culprit can even be the target species (e.g. scree skinks, *O. waimatense*, may eat other lizards caught in traps; Lettink unpublished data). Additionally, traps used for long-term monitoring must be properly disabled when not in use (e.g. filled with rocks or other non-perishable and climbable material and by using tight-fitting lids); unused pitfalls can degrade/rust over time and become 'death' traps.

Pitfall traps can be used for surveys but are especially suited to long-term monitoring since they can remain in the ground between trapping sessions (Greene and McNutt 2012). In New Zealand, pitfall traps are typically used with bait added as an attractant (most often pear in canned or pureed form; Whitaker 1967) and without drift fences, which are generally deployed elsewhere in the world to guide animals into (non-baited) traps (McDiarmid et al. 2012). This difference in deployment is attributable to the late Tony Whitaker, a prominent New Zealand herpetologist who pioneered and promoted the use of baited pitfall traps (Whitaker 1967, 1994). Although baiting traps is much quicker and easier than the laborious process of installing drift fences, it is not always effective (Perrott et al. 2011) or advisable because it may attract predators (small mammals and ants are particularly problematic).

Other baits used with variable success to entice New Zealand lizards into live traps include sardines, cat food, soil, live invertebrates, honey, aniseed, various fresh and canned fruits, and artificial banana and raspberry lures (Patterson 1992; Gebauer 2009; Whitaker 1994; Perrott et al. 2011; H. Jamieson, pers. comm.). In general, bait appears to increase capture rates of New Zealand lizards (but see Perrott et al. 2011).

10.3.2 Funnel Traps

A funnel trap consists of a cylinder with an inverted funnel attached to one or both ends (Vogt 1941). They are commonly made of plastic, nylon or metal mesh, the latter being the most robust. Enticed by bait (as for pitfall traps) or guided by drift fencing, lizards enter traps by climbing through the funnel mouth and are subsequently unable to relocate the narrow opening to escape. Funnel traps should be positioned so that lizards are easily able to locate their openings (Christiansen and Vandewalle 2000) and shaded to avoid overheating (Thompson and Thompson 2010).

A prevalent design used in New Zealand is the ‘Gee’s minnow trap (MT28 fish trap; Pentair Aquatic Ecosystems, USA), which is a double-ended galvanised wire trap designed to capture fish (Fig. 10.1). These traps were first used in 2002 on Great Barrier Island to enhance capture rates of chevron skinks (*O. homalonotum*), which were not readily caught in pitfall traps (H Jamieson, pers. comm.). Funnel traps, including cheaper and smaller designs, have since been used to sample lizards nationwide (e.g. Barr 2009; Gebauer 2009; Patterson and Bell 2009). A novel New Zealand design, which consists of a mesh bin with a funnel placed inside that is deployed upright in vegetation (Fig. 10.1) has proven particularly useful for capturing elusive Cook Strait striped geckos (*Toropuku stephensi*; Burbidge 2015; L. Moran, pers. comm.).

10.3.3 Adhesive Traps

Adhesive (also known as glue or sticky) traps are highly effective for sampling terrestrial and arboreal lizards (Bauer and Sadlier 1992; Rodda et al. 2005); however, their use for trapping of vertebrates is currently restricted in New Zealand. They are easily made from commercially available mouse traps, which consist of stiff boards with an adhesive side (Fig. 10.1). Adhesive traps may be placed flat on the ground, folded into a tunnel or wrapped around tree branches and trunks. Some brands are impregnated with 'attractive' artificial scents, and bait (e.g. banana) can also be used to attract lizards. Animals stuck on traps are carefully removed with the application of vegetable oil, which dissolves the adhesive.

Adhesive traps are inexpensive, effective and easy to use, but can incur high mortality rates (Table 10.1). Lizards stuck on traps are vulnerable to predation, dehydration, heat stress and injury during removal (McDiarmid et al. 2012). In addition, traps may adhere to and be carried off by larger animals (e.g. rodents), and invertebrate by-catch is unavoidable. In New Zealand, adhesive trapping of vertebrates is only permitted for licensed pest control operators and for some biosecurity applications (e.g. a recent attempt to eradicate invasive plague skinks, *Lampropholis delicata*, from Great Barrier Island; Wairepo 2015; Chapple et al. 2016).

10.4 Artificial Retreats

Artificial retreats (also known as cover boards or artificial cover objects) are objects that are deliberately placed in the field to attract lizards and other herpetofauna by providing shelter, protection from predators and/or thermoregulation opportunities. When retreats are inspected, animals are counted or captured by hand. Depending on the tendency of the target species to use cover objects, their fidelity to natural retreats and the availability of natural retreats in the surrounding habitat, a placement period of weeks or months may be required before lizards will consistently use artificial retreats (Lettink and Cree 2007).

Artificial retreats are one of the most widespread and common tools for sampling herpetofauna worldwide, particularly for snakes and lizards (e.g. Webb and Shine 2000; Croak et al. 2010) and terrestrial salamanders (Fellers and Drost 1994; Marsh and Goicochea 2003). Designs range in complexity, and materials used can include wood, tiles, concrete, corrugated iron and Onduline (a roofing and cladding product), felt, carpet, plastic, cardboard and closed-cell foam (McDiarmid et al. 2012; Nordberg and Schwarzkopf 2015).

Most designs are easy to use and relatively inexpensive (≤NZ$5 each), but construction may require some time and effort. Since animals enter and exit artificial retreats of their own volition, risk of mortality is lower than for live trapping. However, as for any sampling device that is left in the field, there is a risk of accidental or deliberate interference (Table 10.1), including vandalism (Webb and Shine 2000) and poaching. For example, as part of a study on five-lined skinks (*Eumeces fasciatus*) in Canada, researchers asked pet shops if they were willing to sell (illegally collected) animals; in one case, they were told they could save money by sourcing the animals themselves and were given directions to one of their own study plots, which contained artificial microhabitats (Hecnar and M'Closkey 1998).

Novel artificial retreat designs have been developed for New Zealand lizards. These designs include closed-cell foam covers mounted in trees (Bell 2009), and Onduline placed on the ground in single or multiple layers (Fig. 10.1; Lettink and Cree 2007; O'Donnell and Hoare 2012). Such designs have increased encounter rates of visually cryptic species that are difficult to detect by other means (e.g. harlequin gecko, *Tukutuku rakiurae*; M Tocher, pers. comm.), but are not useful for instantaneous surveys or for sampling *Naultinus* geckos (Lettink and Monks 2016).

Artificial retreats should be checked under optimal weather conditions for the target species (e.g. Hoare et al. 2009) and be calibrated to ensure that index counts reflect abundance (Lettink et al. 2011). In addition to weather conditions and retreat design, occupancy of artificial retreats by herpetofauna may be affected by retreat size (O'Donnell and Hoare 2012), density (Reading 1997), placement period (Batson et al. 2015), sampling frequency (Wilson et al. 2007) and microhabitat features (Chavel et al. 2012). A thorough understanding of microhabitat selection, including preferred temperatures of the target species, is vital when developing new designs (Thierry et al. 2009; Croak et al. 2008, 2010). Further research is needed to define optimal sampling conditions for a range of species in different habitats. Design modifications that reduce predation risk to lizards (e.g. by small mammals, such as mice, entering retreats in search of prey or shelter) are also important.

10.5 Lizard Sign: Camera Stations and Footprint Tracking

Determining the presence of lizards does not always require capture or direct observation; sign encountered in the field may provide the first indication of lizard presence. This can include sloughed skin fragments, characteristic uric acid tipped faeces (Whitaker 1994), vocalisations, footprints or tracks, and images of lizards taken by camera stations. Lizard sign is deliberately sought in herpetological surveys (e.g. during systematic searches) but may also be incidentally encountered whilst sampling other faunal groups. This section describes two relatively new field methods originally developed for mammals that are currently under investigation for sampling lizards: camera stations and footprint tracking.

10.5.1 Camera Stations

Camera stations record images of animals passing through a camera's field of view and store these in digital format for subsequent viewing. Thus, the observer is replaced by an unmanned camera. Camera stations are best placed in frequently used areas (e.g. basking or egg-laying sites) and may be coupled with bait to attract the species of interest. Cameras can be programmed to record continuously or to take still photographs, either at predefined times or when triggered by sensors or pressure plates (O'Connell et al. 2011). Camera height, image size, and other settings need to be optimised for the size of the target species (Glen et al. 2013). They have been effective for sampling large herpetofauna (e.g. varanid lizards; Ariefiandy et al. 2013).

The advantages and disadvantages of this method are listed in Table 10.1. In general, camera stations are noninvasive and capable of continuous monitoring, thereby reducing time and effort in the field (O'Connell et al. 2011). They can record behaviours that would be difficult or impossible to observe directly (e.g. behaviour of basking pregnant geckos, *Woodworthia* 'Otago large', in the field; Gibson et al. 2015). However, trials on New Zealand species reported low detection rates compared to visual searching and significant time requirements for viewing images (Johnston 2014; Bogish 2014). Technological advances are expected to improve the utility of camera stations for sampling lizards in the wild; however, the small size of New Zealand species limits the use of camera stations for monitoring. At present, camera stations are best used for gathering other biological data, such as lizard behaviour, or for advocacy (e.g. webcams).

10.5.2 Footprint Tracking

Lizard presence may be revealed by footprints left on fine sand, track stations (fixed plots constructed to collect animal tracks; McDiarmid et al. 2012) or custom-made tracking cards placed in tunnels or other structures (e.g. bamboo hides; Vencatasamy 2015). New Zealand lizards are mostly too small to leave definitive tracks in sand, rendering track stations ineffective. However, footprint tracking using a modified tracking-card-and-tunnel system has become an effective detection tool, in some cases also permitting species identification.

Tracking tunnels (King and Edgar 1977) are routinely used in New Zealand to detect and measure the activity of introduced mammalian predators, especially rodents and mustelids. Footprints are acquired when animals, enticed by suitable bait placed inside the tunnel, walk over a pre-inked card or ink tray placed on the tunnel floor. Animals are identified to species or genus from the patterns and sizes of their footprints, either by eye or with the aid of automated track recognition software (e.g. Russell et al. 2009).

Tracking tunnels pose no risk of mortality, can be left in the field to obtain tracks until the ink dries (generally ≤ 2 weeks) and require only modest efforts to operate (Table 10.1). These advantages, coupled with incidental observations of lizard footprints obtained during pest-mammal monitoring, have stimulated research exploring the utility of this method for sampling New Zealand lizards. For example, a small remnant population of Raukawa (formerly 'common') geckos, *W. maculata*, was discovered on Tiritiri Matangi Island near Auckland by the presence of footprints left in rodent tracking tunnels (Baling et al. 2013).

Footprint identification keys have been developed for a subset of New Zealand lizard species (Siyam 2006) by modifying standard protocols for pest-mammal tracking (Gillies and Williams 2013). These modifications include the use of coarser cards and lower-viscosity ink. Species identification is not possible for closely related, similar-sized species living in sympatry and is generally more difficult for skinks than geckos (Jarvie and Monks 2014).

Several studies have compared the detectability of New Zealand lizards using footprint tracking with that of other sampling methods (Siyam 2006; van Winkel 2008; McClure 2011). Footprint tracking, spotlighting and artificial refuges were used to detect Duvaucel's geckos following translocation, with footprint tracking the only method to provide regular and reliable confirmation of species' presence throughout the monitoring period (van Winkel 2008). Conversely, for terrestrial skinks, no significant difference in their detectability was observed between footprint tracking, pitfall trapping and funnel trapping (McClure 2011).

Further research, including sampling a greater range of species in additional habitats, and calibration against known densities (Siyam 2006; Rodda 2012), is required to determine the accuracy and precision of footprint tracking for lizard monitoring. Modifications to this technique that permit sampling of arboreal lizards are also worth pursuing (e.g. the Eaves Monitoring System; https://vimeo.com/54271219). A novel electronic footprint sensor pad system (PAWS: Print Acquisition for Wildlife Surveillance) under development for pest mammals in New Zealand has the potential to simultaneously record lizard encounters (Blackie and Muchna 2015). Regardless, footprint tracking has proven its value as a detection tool for lizards and can also be used for species identification in some areas (e.g. http://www.rotokare.org.nz/uploaded_images/Education/Identifying-animal-tracks.pdf).

10.6 Detector Dogs

Dogs have a highly developed olfactory sense and can be trained to indicate the presence of reptiles by performing a trained alert (e.g. sitting), or via changes in their natural body language (Cablk and Heaton 2006; Browne et al. 2015). Detector dogs are used in biosecurity (e.g. searching cargo leaving Guam for invasive brown tree snakes, *Boiga irregularis*; Engeman et al. 1998) and for conservation purposes (Cablk and Heaton 2006). Under controlled conditions, dogs were able to identify reptile scent and sign, including that of tuatara, *Sphenodon punctatus*, and native lizards (Browne et al. 2015). However, in the field they must be able to accurately and reliably identify the target scent whilst ignoring all other odours encountered, including that of other, similar species (Cablk and Heaton 2006).

In New Zealand, lizard detector dogs were first trialled in 2002 with the aim of improving detection rates of rare and cryptic species, including chevron skink, and harlequin and alpine geckos (*Mokopirirakau* spp.; M. Tocher, pers. comm.). To work with protected wildlife (including native lizards), dog-and-handler teams must pass a two-stage certification process under DOC's Conservation Dogs Programme. Although detector dogs are sometimes useful, their utility in the field is limited by aspects of lizard behaviour (Table 10.1). For example, emerged lizards found by a detector dog tend to react by seeking cover, and subsequent recovery of the animal by the handler is not always possible. Overall, lizard detector dogs are most valuable in surveys of terrestrial habitats occupied by species that are not easily located by other means, particularly where lizards are scarce and easy to recover. Formal trials comparing the accuracy of detector dogs compared with human observers (e.g. Cablk and Heaton 2006) are needed to determine the ultimate value of this method for lizards.

10.7 Methods Used for Individual Identification

Much herpetological research, including monitoring, is not possible without some sort of method to individually identify animals. Put simply, without individual identification (ID), there would be no long-term data on survival, home range, movements, longevity, reproductive output and many other important biological measures. Identification methods can be temporary or permanent (i.e. used to identify individuals for their entire lifespan), and many different methods have been trialled, with varying results (Table 10.2). Here, we provide in-depth information on three commonly used ID methods for New Zealand lizards: temporary marking and two methods of permanent marking/ID (photo-ID and toe-clipping). Of interest, a recent attempt to develop an alternate permanent marking method to toe-clipping for New Zealand lizards (micro-branding; Table 10.2) was unsuccessful (Hitchmough et al. 2012). For permanent marking methods to be successful, the marks must remain legible for the duration of an animal's lifespan: no mean feat given the extreme longevity of native lizards (see Cree and Hare 2016).

10.7.1 Temporary Marking

Temporary marking involves the application of dots, numbers, patterns or other marks to predefined regions of lizards using non-toxic paint, dye, nail varnish, correction fluid or ink (Patterson 1992; Beausoleil et al. 2004). Marks may be

Table 10.2 Methods for individual identification of lizards that have been trialled in New Zealand

Marking method	Description	Species trialled	Outcome	Source(s)
[a]Micro-branding	Numeric code of spot brands (hot or cold) applied to the body and/or limbs	*Woodworthia maculata* ($N = 20$)	• Slow to heal; no evidence of brand-related mortality or increased parasite load • Brands faded, remaining readable in only 29 % of geckos after 3 years	Hitchmough et al. (2012)
		Oligosoma aeneum ($N = 10$)	• Slow to heal; no evidence of brand-related mortality or increased parasite loads • Brands faded rapidly and difficult to read after 3 months; unreadable after 2.5 years	Hitchmough et al. (2012)
Passive Integrated Transponder (PIT) tags	PIT tags inserted subcutaneously in the same location on all sample animals using a PIT tag applicator gun (e.g. Allflex®)	*Hoplodactylus duvaucelii* ($N = 19$ and $N = 20$)	• Only used in geckos with SVL > 115 mm • Animals translocated to two islands • Tag loss (or loss of tag function) has occurred in one individual (D. van Winkel pers. comm.) • Monitoring on-going	van Winkel (2008)
Photo identification	Identification of individuals from natural marks or other features. High-resolution, standardised photos are taken of individuals and compared to images archived in a digital photo-library, either manually (by eye) or using computer software programmes	*Naultinus gemmeus* ($N = 15$)	• Accuracy rate 100 % • Manual photo-matching	Knox et al. (2013)
		Naultinus gemmeus ($N = 1600$)	• Matching success 99.5 % • Computer matching (SLOOP)	Duyck et al. (2015)
		Oligosoma grande ($N = 2500$)	• Matching success 99 % • Computer matching (SLOOP)	Duyck et al. (2015)
		Oligosoma otagense ($N = 900$)	• Matching success 96 % • Computer matching (SLOOP)	Duyck et al. (2015)

(continued)

Table 10.2 (continued)

Marking method	Description	Species trialled	Outcome	Source(s)
		Oligosoma microlepis (*N* = 30)	• Accuracy rate 88.1 % • Manual matching	Gebauer (2009)
		Oligosoma judgei (*N* = 10)	• Accuracy rate 92.9 % • Manual matching	Johnston (2014)
Temporary marking	Application of dots, numbers, patterns or other marks to predefined regions of lizards using various substances	*Oligosoma maccanni* (*N* = 12) and *O. polychroma* (*N* = 2)	• Dorsal patch applied with silver Pilot™ marker, acrylic paint, nail varnish, correction fluid or sheep marker dye • Average mark retention 8–16 days • Recommended low-toxicity paints or dyes	Patterson (1992)
		Oligosoma aff. *polychroma* Clade 5 (*N* = 119)	• Silver Pilot™ xylene-free marker • Number on dorsum of toe-clipped skinks • All marks lost within 1–6 days (Fig. 10.2)	Lettink and O'Donnell (unpub. data)
		Woodworthia chrysosiretica (*N* = 47)	• Silver Pilot™ xylene-free marker • Mark on dorsum of toe-clipped geckos • All marks retained for 29–160 days over winter but lost <36 days in warmer months	Flannagan (2000)
Toe-clipping	Removal of the distal portion of digits in a predetermined combination	*Oligosoma maccanni* (*N* = 118)	• One digit clipped • No effect on recapture probability (cf. temporary marking) during pitfall trapping	Jones and Bell (2010)

Photo-identification has been used in other published research and theses on New Zealand lizards, including *Oligosoma grande* and *O. otagense* (Reardon et al. 2012), *O. chloronoton* (Mules and Hutcheon 2012), *O. homalonotum* (Barr 2009) and *Mokopirirakau* 'southern forest' (Hoare et al. 2013). Other methods listed in Beausoleil et al. (2004) that have not been trialled in New Zealand include hot brands, chemical brands, tattoos and visible (fluorescent and/or elastomer) implants

[a] Method deemed unsuitable for use in New Zealand lizards

SVL = snout-vent length, SLOOP = a computer-based pattern-recognition system

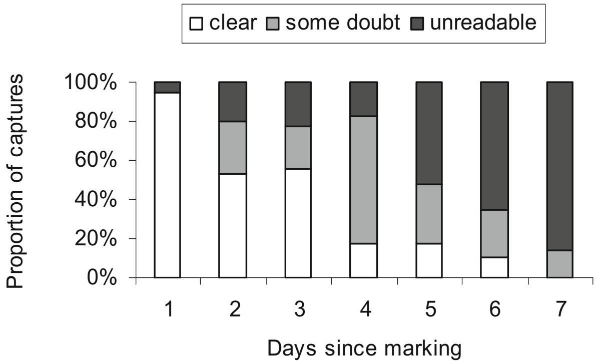


Fig. 10.2 Legibility of temporary marks, written as a numeric code on the dorsum of southern grass skinks, *Oligosoma* aff. *polychroma* Clade 5, using a Silver Pilot^{TM} xylene-free marker. Legibility reduced quickly over 7 days of monitoring. Skinks ($N = 119$) were captured in pitfall traps in the Eglinton Valley, Fiordland, January 2007, and were also toe-clipped as a secondary means of identification. Lettink and O'Donnell (Unpublished data)

applied to lizards in order to identify individuals (e.g. numbers written on the ventral surface of individuals; Jones and Bell 2010) or 'batch-mark' animals to simply show they have been previously encountered (e.g. dot of correction fluid on the head; Towns 2002). The most widely used temporarily mark applied in studies of New Zealand lizards is a unique number written on the dorsal or ventral surface using a non-toxic, permanent marker (e.g. Pilot xylene-free pen; Patterson 1992; Flannagan 2000; Jones and Bell 2010). Xylene is toxic to vertebrates and should be avoided (Beausoleil et al. 2004).

Although application of temporary marks is generally quick and easy, they may increase the conspicuousness of an individual to predators and can be lost within a day due to abrasion or shedding of the skin (this may occur several times over summer; Whitaker 1982). For example, retention of numbers applied to the dorsum with a silver Pilot xylene-free pen varied from 1–6 days in terrestrial *Oligosoma* skinks (Fig. 10.2) to 160 days in arboreal goldstripe geckos, *W. chrysosiretica* (Table 10.2; Flannagan 2000). Whether rate of mark loss is related to habit or taxon per se is unknown, but is likely a combination of both. The accuracy of this method can be improved by frequent reapplication of marks (where animals are recaptured regularly) or double marking using a second, independent method.

10.7.2 Photo-Identification

Photo-ID is where individual animals are identified using natural marks or other features (e.g. scale shapes and patterns, iris patterns; Rocha et al. 2013; Duyck et al. 2015). It requires taking high-resolution, standardised photographs of a predefined region(s) of each individual encountered during a sampling session and comparing these with previous photographs archived in a photo-library. It can be completely noninvasive when combined with visual searching (e.g. Reardon et al. 2012) and minimally intrusive when used with other sampling techniques (i.e. where some handling will be required). As the method is minimally invasive, it has become a popular alternative to toe-clipping for identifying New Zealand lizards; to date, accuracy rates have been published for six species (Table 10.2).

One of the main advantages of photo-ID is that, when used without capture (i.e. photo-resight rather than mark-recapture methods), the ability to monitor populations effectively is not compromised by the effects of direct disturbance or capture on subsequent capture probabilities. Reducing disturbance is of particular importance when assessing population survival or abundance (Reardon et al. 2012). In general, photo-ID is best employed for monitoring small populations that occupy well-defined areas (Beausoleil et al. 2004). However, photo-ID can be very time consuming and cannot be used for species that lack distinguishing marks (Rocha et al. 2013). Animal handling and/or identification times are typically longer than those of other permanent marking methods (e.g. toe-clipping) and accuracy is not always 100 % (Table 10.2). In addition, photo-resight methods do not permit collection of other biological information (e.g. size, reproductive condition, mass).

Photo-matching was historically done by eye, but pattern-recognition software (e.g. the free Interactive Individual Identification System (I^3S); Van Tienhoven et al. 2007) is increasingly used. The software package SLOOP (Duyck et al. 2015), an image-retrieval system that incorporates crowd-sourced relevance feedback, has been successfully trialled on several New Zealand lizard species (Table 10.2). Pattern-recognition software does not necessarily increase accuracy, but it does improve efficiency and facilitates monitoring of large populations (Gamble et al. 2008; Duyck et al. 2015).

10.7.3 Toe-Clipping

Toe-clipping entails the removal of the distal portion of toes (usually 2–4 digits) below the nail bed in predetermined combinations. Generally, the clipped digits are on different feet and any natural toe loss is incorporated. Operators should be experienced and use clean and sharp tools. Whilst toe-clipping is quick, cheap and easy, it is no longer the standard method for permanent marking of New Zealand lizards due to animal welfare concerns and negative public perception of the practice (Beausoleil et al. 2004; Mellor et al. 2004; Perry et al. 2011).

Nonetheless, toe-clipping has been essential for long-term studies of New Zealand lizards (e.g. Anastasiadis and Whitaker 1987; Bannock et al. 1999; Hare and Cree 2005). In fact, without the use of toe-clipping by early researchers, and their excellent record-keeping, interesting and important details on the biology of New Zealand lizards would remain unknown. For example, many species demonstrate extreme longevity (30+ years; Bannock et al. 1999) and delayed maturity (Cree and Hare 2016), and some geckos have biennial reproduction

(Cree and Guillette 1995). These data are vital for accurate conservation management, especially during translocations (Towns and Broome 2003). In addition, toe-clipping has the added benefit of providing tissue for genetic studies.

Globally, studies of the effects of toe-clipping on lizards generally show no negative impact on the variables examined. For example, toe-clipping had no effect on recapture probability (cf. individuals who did not have their toes clipped) of McCann's skinks, *O. maccanni*, caught in pitfall traps (Jones and Bell 2010), induced a lower stress-hormone response than handling alone in Australian lizards (Langkilde and Shine 2006), had limited to no effect on locomotor performance and survival in many species (e.g. Borges-Landaez and Shine 2003) and did not lessen climbing ability in the arboreal gecko *Hemidactylus turcicus* (Paulissen and Meyer 2000). However, it did reduce clinging ability in the lizard *Anolis carolinensis*, and this was correlated to the numbers of toes that were clipped on the forelimbs (two = 40 % reduction; four = 60 % reduction; Bloch and Irschick 2004). Regardless of the pros and cons of toe-clipping, its use (and that of any permanent marking method) should be well justified and only employed where necessary.

10.8 Conclusions

Effective sampling of New Zealand lizards requires appropriate field methods coupled with a thorough understanding of the behaviour and ecology of the target species, including its thermal physiology (Hare and Cree 2016), activity phase, movements, bait preferences and interaction with sampling devices. Knowledge of refuge use is also important, particularly where lizards coexist with introduced mammalian predators (Towns et al. 2016; Nelson et al. 2016), as this may determine where sampling is conducted. The methods described above collectively permit sampling of most New Zealand lizard species. New and/or improved sampling methods are needed for arboreal species, particularly those living in tall forest (e.g. striped skink and *Mokopirirakau* geckos), and visually cryptic taxa that are not enticed by traps or artificial retreats (e.g. *Naultinus* geckos). Footprint tracking appears promising, but needs further refinement. Another priority is further investigation of ethically acceptable, accurate and fast permanent marking methods.

Acknowledgements We thank Dylan van Winkel, Halema Jamieson, Les Moran and Mandy Tocher for their personal communications, Trent Bell and Les Moran for supplying photographs, Colin O'Donnell for the use of his unpublished data and Riki Mules and David Chapple for useful suggestions on an earlier draft of this chapter. Table 10.1 is derived, in part, from an article in the Journal of the Royal Society of New Zealand (Lettink and Monks 2016).

References

Anastasiadis JM, Whitaker AH (1987) Longevity of free-living *Hoplodactylus maculatus* (Reptilia: Gekkonidae). N Z J Ecol 10:141–142

Ariefiandy A, Purwandana D, Seno A, Ciofi C, Jessop TS (2013) Can camera traps monitor Komodo dragons a large ectothermic predator? PLoS One 8(3):e58800

Baling M, Van Winkel D, Rixon M, Ruffell J, Ji W, Ussher G (2013) A review of reptile research and conservation management on Tiritiri Matangi Island, New Zealand. N Z J Ecol 37:272–281

Bannock CA, Whitaker AH, Hickling GJ (1999) Extreme longevity of the common gecko (*Hoplodactylus maculatus*) on Motunau Island, Canterbury, New Zealand. N Z J Ecol 23:101–103

Barr BP (2009) Spatial ecology, habitat use, and the impacts of rats on chevron skinks (*Oligosoma homalonotum*) on Great Barrier Island. Unpublished MSc thesis, Massey University, Auckland

Batson WG, O'Donnell CFJ, Nelson NJ, Monks JM (2015) Placement period of artificial retreats affects the number and demographic composition but not the body condition of skinks. N Z J Ecol 39:273–279

Bauer AM, Sadlier RA (1992) The use of mouse glue traps to capture lizards. Herpetol Rev 23:112–113

Beausoleil NJ, Mellor DJ, Stafford KJ (2004) Methods for marking New Zealand wildlife: amphibians, reptiles and marine mammals. New Zealand Department of Conservation, Wellington

Bell TP (2009) A novel technique for monitoring highly cryptic lizard species in forests. Herpetol Conserv Biol 4:415–425

Blackie H, Muchna K (2015) PAWS: a novel technology for lizard detection and monitoring, Department of Conservation research & development series 347. New Zealand Department of Conservation, Wellington

Bloch N, Irschick DJ (2004) Toe-clipping dramatically reduces clinging performance in a pad-bearing lizard (*Anolis carolinensis*). J Herpetol 37:293–298

Bogish M (2014) Comparing the use of time-lapse photography and visual observations for post release monitoring of Otago skinks. Unpublished wildlife management report no. 276, University of Otago, Dunedin

Borges-Landaez PA, Shine R (2003) Influence of toe-clipping on running speed in *Eulamprus quoyii*, an Australian scincid lizard. J Herpetol 37:592–595

Browne CM, Stafford KJ, Fordham RA (2015) The detection and identification of tuatara and gecko scents by dogs. J Vet Behav Clin Appl Res 10:496–503

Burbidge SJ (2015) Estimating detectability, population size and habitat use of the vulnerable Cook Strait striped gecko (*Toropuku stephensi*). Unpublished thesis. Bangor University, Wales

Cablk ME, Heaton JS (2006) Accuracy and reliability of dogs in surveying for desert tortoise (*Gopherus agassizii*). Ecol Appl 16:1926–1935

Chapple DG, Reardon JT, Peace JE (2016) Origin, spread and biology of the invasive plague skink (*Lampropholis delicata*) in New Zealand. Chap. 13. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chavel EE, Hoare JM, Batson WH, O'Donnell CFJ (2012) The effect of microhabitat on skink sightings beneath artificial retreats. N Z J Zool 39:71–75

Christiansen JL, Vandewalle T (2000) Effectiveness of three trap types in drift fence surveys. Herpetol Rev 31:158–160

Cree A, Guillette LJ Jr (1995) Biennial reproduction with a fourteen-month pregnancy in the gecko *Hoplodactylus maculatus* from southern New Zealand. J Herpetol 29:163–173

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Croak BM, Pike DA, Webb JK, Shine R (2008) Three-dimensional crevice structure affects retreat site selection by reptiles. Anim Behav 76:1875–1884

Croak BM, Pike DA, Webb JK, Shine R (2010) Using artificial rocks to restore non-renewable shelter sites in human-degraded systems: colonization by fauna. Restor Ecol 18:428–438

Duyck J, Finn C, Hutcheon A, Vera P, Salas J, Ravela S (2015) Sloop: a pattern retrieval engine for individual animal identification. Pattern Recognit 48:1059–1073

Engeman RM, Vice DS, Rodriguez DV, Gruver KS, Santos WS, Pitzler ME (1998) Effectiveness of detector dogs for locating brown tree snakes in cargo. Pac Conserv Biol 4:348–353

Fellers GM, Drost CA (1994) Sampling with artificial covers. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS (eds) Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, DC, pp 146–150

Flannagan HJ (2000) Conservation biology of the Goldstripe Gecko (*Hoplodactylus chrysosireticus*) and Interactions with Duvaucel's Gecko (*Hoplodactylus duvaucelii*) on Mana Island, Cook Strait, New Zealand. Unpublished MSc thesis, Massey University, Palmerston North

Gamble L, Ravela S, McGarigal K (2008) Multi-scale features for identifying individuals in large biological databases: an application of pattern recognition technology to the marbled salamander *Ambystoma opacum*. J Appl Ecol 45:170–180

Gebauer K (2009) Trapping and identification techniques for small-scaled skinks (*Oligosoma microlepis*), Research and development series 318. New Zealand Department of Conservation, Wellington

Gibson S, Penniket S, Cree A (2015) Are viviparous lizards from cool climates ever exclusively nocturnal? Evidence for extensive basking in a New Zealand gecko. Biol J Linn Soc 115:882–895

Gillies CA, Williams D (2013) DOC tracking tunnel guide v2.5.2: using tracking tunnels to monitor rodents and mustelids. New Zealand Department of Conservation, Hamilton

Glen AS, Cockburn S, Nichols M, Ekanayake J, Warburton B (2013) Optimising camera traps for monitoring small mammals. PLoS One 8(6):e67940

Greene T, McNutt K (2012) Biodiversity inventory and monitoring toolbox. New Zealand Department of Conservation, Wellington. http://www.doc.govt.nz/biodiversitymonitoring/

Guyer C, Donnelly MA (2012) Visual encounter surveys. In: McDiarmid RW, Foster MS, Guyer C, Whitfield Gibbons J, Chernoff N (eds) Reptile biodiversity: standard methods for inventory and monitoring. University of California Press, Berkeley, CA, pp 218–220

Hare KM, Cree A (2005) Natural history of *Hoplodactylus stephensi* (Reptilia: Gekkonidae) on Stephens Island, Cook Strait, New Zealand. N Z J Ecol 29:137–142

Hare KM, Cree A (2016) Thermal and metabolic physiology of New Zealand lizards. Chap. 9. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hecnar SJ, M'Closkey RT (1998) Effects of human disturbance on five-lined skink, *Eumeces fasciatus*, abundance and distribution. Biol Conserv 85:213–222

Hitchmough R, Neilson K, Goddard K, Goold M, Gartrell B, Cockburn S, Ling N (2012) Assessment of microbranding as an alternative marking technique for long-term identification of New Zealand lizards. NZ J Ecol 36:151–156

Hitchmough RA, Patterson GB, Chapple DG (2016a) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hitchmough R, Barr B, Lettink M, Monks J, Reardon J, Tocher M, van Winkel D, Rolfe J (2016b) Conservation status of New Zealand reptiles, 2015. New Zealand Department of Conservation, Wellington

Hoare JM, Adams LK, Bull LS, Towns DR (2007) Attempting to manage complex predator–prey interactions fails to avert imminent extinction of a threatened New Zealand skink population. J Wildl Manage 71:1576–1584

Hoare JM, O'Donnell CFJ, Westbrooke I, Hodapp D, Lettink M (2009) Optimising the sampling of skinks using artificial retreats based on weather conditions and time of day. Appl Herpetol 6:379–390

Hoare JM, Melgren P, Chavel EE (2013) Habitat use by southern forest geckos (*Mokopirirakau* 'Southern Forest') in the Catlins, Southland. N Z J Zool 40:129–136

Jarvie S, Monks JM (2014) Step on it: can footprints from tracking tunnels be used to identify lizard species? N Z J Zool 41:210–217

Johnston L (2014) Trials and evaluations of monitoring tools for New Zealand's alpine skinks: the Barrier skink (*Oligosoma judgei*) and the Sinbad skink (*O. pikitanga*). Unpublished Postgraduate Diploma of Wildlife dissertation, University of Otago, Dunedin

Jones C, Bell T (2010) Relative effects of toe-clipping and pen-marking on short-term recapture probability of McCann's skinks (*Oligosoma maccanni*). Herpetol J 20:237–241

King CM, Edgar RL (1977) Techniques for trapping and tracking stoats (*Mustela erminea*); a review, and a new system. N Z J Zool 4:193–212

Knox CD, Cree A, Seddon PJ (2013) Accurate identification of individual geckos (*Naultinus gemmeus*) through dorsal pattern differentiation. N Z J Ecol 37:60–66

Langkilde T, Shine R (2006) How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. J Exp Biol 209:1035–1043

Lettink M, Cree A (2007) Relative use of three types of artificial retreats by terrestrial lizards in grazed coastal shrubland, New Zealand. Appl Herpetol 4:227–243

Lettink M, Monks JM (2016) Survey and monitoring methods for New Zealand lizards. J R Soc N Z 46:16–28

Lettink M, O'Donnell CFJ, Hoare JM (2011) Accuracy and precision of skink counts from artificial retreats. N Z J Ecol 35:236–246

Marsh DM, Goicochea MA (2003) Monitoring terrestrial salamanders: biases caused by intense sampling and choice of cover objects. J Herpetol 37:460–466

Mazerolle MJ (2003) Using rims to hinder amphibian escape from pitfall traps. Herpetol Rev 34:213–215

McClure C (2011) Testing translocation, detection and live trapping methods for New Zealand lizards. Unpublished BSc honours dissertation. Lincoln University, Lincoln

McDiarmid RW, Foster MS, Guyer C, Whitfield Gibbons J, Chernoff N (eds) (2012) Reptile biodiversity: standard methods for inventory and monitoring. University of California Press, Berkeley, CA

Mellor DJ, Beausoleil NJ, Stafford KJ (2004) Marking amphibians, reptiles and marine mammals: animal welfare, practices and public perceptions in New Zealand. New Zealand Department of Conservation, Wellington

Mules RD, Hutcheon A (2012) *Oligosoma chloronoton* (green skink) longevity, site fidelity. Herpetol Rev 43:488–489

Nelson NJ, Romijn RL, Dumont T, Reardon JT, Monks JM, Hitchmough RA, Empson R, Briskie JV (2016) Lizard conservation in mainland sanctuaries. Chap. 12. In: Chapple DG (ed) - New Zealand lizards. Springer, Cham

Newman DG (1994) Effects of a mouse, *Mus musculus*, eradication and habitat change on lizard populations of Mana Island, New Zealand, with special reference to McGregor's skink, *Cyclodina macgregori*. N Z J Zool 21:443–456

Nordberg EJ, Schwarzkopf L (2015) Arboreal cover boards: using artificial bark to sample cryptic arboreal lizards. Herpetologica 71:268–273

O'Connell AF, Nichols JD, Karanth UD (eds) (2011) Camera traps in animal ecology: methods and analysis. Springer, Tokyo

O'Donnell CFJ, Hoare JM (2012) Monitoring trends in skink sightings from artificial retreats: influence of retreat design, placement period, and predator abundance. Herpetol Conserv Biol 7:58–66

Patterson GB (1992) Development of Otago skink and grand skink population census and monitoring techniques. Science & Research internal report no. 133. New Zealand Department of Conservation, Wellington

Patterson G, Bell T (2009) The Barrier skink *Oligosoma judgei* n. sp. (Reptilia: Scincidae) from the Darran and Takitimu Mountains, South Island, New Zealand. Zootaxa 2271:43–56

Paulissen MA, Meyer HA (2000) The effect of toe-clipping on the gecko *Hemidactylus turcicus*. J Herpetol 34:282–285

Perrott J, Schragen S, Thoresen J, Jayasinghe A (2011) Speckled skink bait experiments on Mokoia Island, Lake Rotorua. N Z J Zool 38:276–277

Perry G, Wallace MC, Perry D, Curzer H, Muhlberger P (2011) Toe-clipping of amphibians and reptiles: science, ethics, and the law. J Herpetol 45:547–555

Pike DA, Croak BM, Webb JK, Shine R (2010) Subtle—but easily reversible—anthropogenic disturbance seriously degrades habitat quality for rock-dwelling reptiles. Anim Conserv 13:411–418

Reading CJ (1997) A proposed standard method for surveying reptiles on dry lowland heath. J Appl Ecol 34:1057–1069

Reardon JT, Whitmore N, Holmes KM, Judd LM, Hutcheon AD, Norbury G, Mackenzie DI (2012) Predator control allows critically endangered lizards to recover on mainland New Zealand. N Z J Ecol 36:141–150

Rocha R, Carrilho T, Rebelo R (2013) Iris photo-identification: a new methodology for the individual recognition of Tarentola geckos. Amphibia-Reptilia 34:590–596

Rodda GH (2012) Statistical properties of techniques and validation. In: McDiarmid RW, Foster MS, Guyer CG, Gibbons JW, Chernoff N (eds) Reptile biodiversity: standard methods for inventory and monitoring. University of California Press, Berkeley, CA, pp 197–203

Rodda GH, Dean Bradley K, Fritts TH (2005) Glueboards for estimating lizard abundance. Herpetol Rev 36:252–259

Russell JC, Hasler N, Klette R, Rosenhahn B (2009) Automatic track recognition of footprints for identifying cryptic species. Ecology 90:2007–2013

Siyam SM (2006) Reptile monitoring: development of an effective, passive monitoring technique. Unpublished MSc thesis, University of Auckland, Auckland

Smolensky NL, Fitzgerald LA (2010) Distance sampling underestimates population densities of dune-dwelling lizards. J Herpetol 44:372–381

Thierry A, Lettink M, Besson AA, Cree A (2009) Thermal properties of artificial refuges and their implications for retreat-site selection in lizards. Appl Herpetol 6:307–326

Thompson GG, Thompson SA (2010) Comparative temperature in funnel and pit traps. Aust J Zool 57:311–316

Towns DR (2002) Interactions between geckos, honeydew scale insects and host plants revealed on islands in northern New Zealand, following eradication of introduced rats and rabbits. In: Veitch CR, Clout MN (eds) Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group, Gland and Cambridge, pp 329–335

Towns DR, Broome KG (2003) From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. N Z J Zool 30:377–398

Towns DR, Hitchmough RA, Perrott J (2016) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? Chap. 11. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Van Tienhoven AM, Den Hartog JE, Reijns RA, Peddemors VM (2007) A computer-aided program for pattern-matching natural marks on the spotted raggedtooth shark *Carcharias taurus* (Rafinesque, 1810). J Appl Ecol 44:273–280

van Winkel D (2008) The efficiency of techniques for post-translocation monitoring of the Duvaucel's gecko (*Hoplodactylus duvaucelii*) and evidence of native avian predation on lizards. Unpublished MSc thesis, Massey University, Auckland

Vencatasamy AD (2015) Occupancy, detectability and relative abundance of arboreal geckos using bamboo-hides with ink tracking cards (BH-ITC) on Ile Aux Aigrettes Nature Reserve, Mauritius. Unpublished MSc thesis, Nottingham Trent University

Vogt W (1941) A practical lizard trap. Copeia 1941:115

Wairepo J (2015) Developing biosecurity strategies for an invasive reptile, the plague skink (*Lampropholis delicata*) on Great Barrier Island. MSc thesis, Massey University, Auckland

Webb JK, Shine R (2000) Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles? Biol Conserv 92:93–99

Whitaker AH (1967) Baiting pitfall traps for small lizards. Herpetofauna 23:309–311

Whitaker AH (1968) The lizards of the Poor Knights Islands, New Zealand. N Z J Sci 11:623–651

Whitaker AH (1982) Interim results from a study of *Hoplodactylus maculatus* (Boulenger) at Turakirae Head, Wellington. In: Newman DG (ed) New Zealand herpetology. Proceedings of a symposium held at Victoria University of Wellington, 29–31 Jan 1980, vol 2. New Zealand Wildlife Service Occasional Publication, Wellington, pp 363–374

Whitaker T (1994) Survey methods for lizards. Ecol Manage 2:8–16

Whitaker T, Shaw T, Hitchmough R (1999) Black-eyed geckos (*Hoplodactylus kahuratae*) on Mt Arthur, Kahurangi National Park, Conservation advisory science notes no. 230. New Zealand Department of Conservation, Wellington

Wilson DJ, Mulvey RL, Clark RD (2007) Sampling skinks and geckos in artificial cover objects in a dry mixed grassland-shrubland with mammalian predator control. N Z J Ecol 31:169–185

Chapter 11
Conservation of New Zealand Lizards: A Fauna Not Forgotten but Undervalued?

David R. Towns, Rodney A. Hitchmough, and John Perrott

Abstract Conservation actions are heavily influenced by value judgements and cultural perceptions. The huge lizard fauna of New Zealand played a prominent role in the worldview of the first people (Māori), but appeared to be poorly appreciated by European settlers. Early legislation to protect native fauna explicitly excluded lizards, which remained unprotected until the 1980s. After legislated protection was extended to lizards, the distribution and status of the rarest species have become increasingly understood. About 83 % of the fauna is currently regarded as threatened or at risk. Of the five species included in early recovery plans, two have improved status, two have declined and then improved as management improved and one has declined in listed status, although at least one new population has been established. There is increasing evidence that immediate threats faced by many species can be resolved, particularly those that inhabit islands. Longer-term threats may include genetically compromised populations, extremely protracted monitoring issues and climate change. Threats to progress with lizard conservation also involve socioecological problems such as social attitudes to lizards versus birds and competition for financial resources. Solutions may involve alliances between agencies, academic institutions and Māori organisations, with the latter now including statutory co-management agreements.

Keywords Geckos • Skinks • Māori • Legislation • Threats • Predators • Islands • Translocations • Co-management

---

D.R. Towns (✉)
Department of Conservation, Auckland, New Zealand

Institute for Applied Ecology New Zealand, Auckland University of Technology, Auckland, New Zealand
e-mail: dtowns@doc.govt.nz

R.A. Hitchmough
Department of Conservation, Wellington, New Zealand
e-mail: rhitchmough@doc.govt.nz

J. Perrott
Institute for Applied Ecology New Zealand, Auckland University of Technology, Auckland, New Zealand
e-mail: jperrott@aut.ac.nz

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_11

11.1 Introduction

In the BBC Nature series Prehistoric Life, New Zealand was identified as a land of birds. If the marine avifauna is included and in view of the near absence of terrestrial mammals (other than bats, e.g. King 2005), it seems justified to claim predominance of birds. However, New Zealand is home to another large group of terrestrial vertebrates. With more than 100 identified endemic taxa (Nelson et al. 2014; Hitchmough et al. 2016a, b), the native lizard fauna was historically about equal in size to that of terrestrial and freshwater birds. Although 40 % of the birds have been lost to extinction (Tennyson and Martinson 2006), there are only two (2 %) known recent extinctions of lizards (Worthy 2016), and lizards now represent the highest proportion of native vertebrate terrestrial biodiversity. Furthermore, when corrected for land area, New Zealand probably has the most diverse lizard fauna of any temperate area in the world (Daugherty et al. 1990; Hickson et al. 2000; Chapple et al. 2011). New Zealand could thus reasonably be identified as a land of lizards (Hitchmough et al. 2016b; Chapple and Hitchmough 2016). This diversity of lizards, and their significance, has been so poorly understood that the group has been referred to as a forgotten fauna (e.g. Towns et al. 2001).

The current state of reptile conservation in New Zealand was recently reviewed by Nelson et al. (2014). We aim to complement this review by examining why the contribution of lizards to the terrestrial fauna has historically been overlooked. We acknowledge that conservation is heavily influenced by value judgements and cultural perceptions (Lawton 1997). Since such perceptions have rarely been examined in the New Zealand context, we begin this account with a review of the role of lizards in the world of Māori (also see Shea 2016) through to European contact and into the era of legislated protection. We then explore the reasons why protection was required; the extent and causes of declines faced by many species; measures undertaken to improve the prospects of the fauna, including the development of threat classification systems; the development of recovery plans; and a review of measures used to reverse the declines of selected species. We complete our review with an assessment of the challenges ahead.

11.2 Lizards and the Māori Worldview

The ancestors of today's Māori arrived from Polynesia in about 1280 AD (Wilmshurst et al. 2008), carrying with them cultural traditions developed in the Pacific and East Asia (Anderson et al. 2014). This culture included an array of legends about reptiles, many of which are comprehensively described by Cree (2014), particularly with regard to tuatara (*Sphenodon punctatus*). As Cree points out, her account is derived from published literature and does not attempt to reflect the views of contemporary Māori. We will attempt to partly fill this gap since one of us (JP) is connected to Ngati Whakaue, a subtribe of Te Arawa, has been mentored by his relative John Marsh (a rangatira or chief) and has interviewed several respected Māori authorities about mātauranga (traditional knowledge) of lizards since 1994. These conversations consistently reveal divergence in the ways birds and reptiles, particularly lizards, were viewed. Each species of bird was known to Māori and named, and while tuatara were usually identified as distinct from lizards (Fig. 11.1; see also Cree 2014), the few names for lizards do not reflect the diversity of colours and sizes present. Indeed, we found just one name traditionally used for skinks (Table 11.1). The source of the divergence in Māori attitudes towards birds and lizards is exemplified by the legend of Maui and Hine-nui-te-po (goddess of night and death or guardian of life), versions of which are found throughout Polynesia (Westervelt 1910). A version related to us is as follows. The family of Maui had five brothers, of which the youngest, Mauipotiki, continually flouted tapu (ritual restrictions). As his life neared its end, Maui gathered his brothers to join him in a scheme to destroy Hine-nui-te-po and thereby gain immortality for all

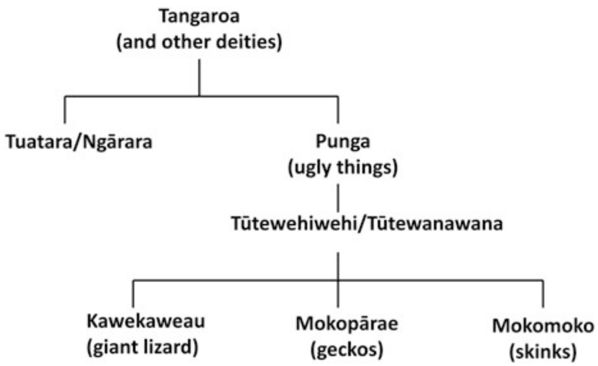


Fig. 11.1 Whakapapa (genealogy) of lizards, modified from Haami (2013), with terminology as in Moorfield (2011). A more detailed whakapapa, including all deity names and their relationship to reptiles, is in Cree (2014)

Table 11.1 Māori words for lizards

Word	Associated species	References
Moko, mokomoko	Generic term for lizard, but particularly skinks	Moorfield (2011)
Niho taniwha	Name for chevron skink used by Ngatiwai	www.ngatiwai.iwi.nz
Moko kākāriki	Green geckos, *Naultinus* spp.	Moorfield (2011) and Cree (2014)
Moko pāpā	Attributed to *Dactylocnemis pacificus* but probably widely used for smaller brown geckos including *Woodworthia maculata*	Moorfield (2011) and cf. Haami (2013)
Moko pārae	Generic for gecko	Moorfield (2011)
Moko pirirākau	Variously attributed to *D. pacificus* (or brown geckos) and forest geckos (*Mokopirirakau granulatus*)	Moorfield (2011), Nielsen et al. (2011) and Haami (2013)
Moko tāpiri	Gecko such as *Woodworthia maculata*	Moorfield (2011)
Kawekaweau	Giant reddish lizard, possibly the extinct gecko *Hoplodactylus delcourti*	Haami (2013)

humankind. As they crept up on the sleeping Hine, Maui warned his brothers to be silent. He would reverse the birth process by entering the body of Hine. When he appeared through her mouth, she would be dead and life would be eternal. To carry out his plan, he changed his brothers into birds and himself into a lizard. As he crawled up Hine's leg, one of the brothers, in the form of piwakawaka (fantail, *Rhipidura fuliginosa*), gave the bird's laughter-like chattering call, which awoke Hine. Thus warned, she crushed Maui between her thighs, ending his life.

Lizards were, to at least some Māori, thus associated with the spirit world, death and tapu (Cree 2014). Even to see a lizard was regarded as predicting misfortune (Cree 2014; Best 2015). On the other hand, lizards commonly appeared in carvings, apparently as guardians of marae (communal meeting houses) and to communicate that a person depicted in the carvings was in the spirit world (Binney 1995). Lizards also appeared in carvings on other buildings, such as pātaka (storehouses) (Cree 2014). Unusually, carvings of lizards were not in stylized form (Best 2015), suggesting an unequivocal warning that proceeding further was forbidden. Lizards and their depiction in carvings may have been associated with warning or dread (Best 2015), but such dread was not universal. Among highborn Māori, lizards could be imbued with great mana (power). The divergent roles of lizards within Māori social structure were illustrated by Stone's (2001) account of a struggle for control of the Auckland isthmus. In this account, the celebrated Waiohua chief, Kiwi Tamaki, boasted that a lizard Rehua-atua (personal protector) within his body would decide his ultimate fate, not mere mortals. When Kiwi Tamaki died in the battle, his foe, Te Waha-akiaki from the Te Taou division of Ngati Whatua, claimed to have liberated the lizard from Kiwi Tamaki's corpse. The lizard Rehua-atua was then captured and eaten by one of the Te Taou, whereupon the offending warrior dropped dead (Stone 2001). Tohunga (esteemed holders of skills and knowledge) may have routinely handled lizards and used them for curing mental and physical illness, as well as for intimidation and power. These acts included sleight of hand, where tohunga appeared to extract lizards from those suffering illness (Cree 2014; Best 2015). Tohunga were also kaitiaki (guardians) of the mauri (life force) of forests. Mauri was often represented by a stone hidden in the forest by tohunga, with a lizard released nearby as guardian. Lizards were also released near burial caves as guardians of the dead and under the corner posts of wānanga (houses of learning; Haami 2013). In addition to differing views about lizards within Māori society, there were likely also regional variations. For example, in some versions of the story of Hine-nui-te-po, Maui is a worm rather than a lizard.

There may also have been temporal changes in attitudes towards lizards. One of us (DRT) has witnessed kuia (matriarchs) of Ngati Hei handling geckos (*Woodworthia maculata*) with great affection when they were presented as evidence of the resurgence of life following the eradication of invasive mammals from Korapuki Island (see also Towns 2002). We have also worked with kuia of Ngati Rehua (a subtribe of Ngatiwai) as kaitiaki for a recovery plan for chevron skinks (*Oligosoma homalonotum*) on Great Barrier Island (see below). Ngatiwai were directly involved in the reintroductions of *Oligosoma macgregori, O. townsi* and

Dactylocnemis pacificus to the Marotiri Islands after the removal of kiore (Pacific rats, *Rattus exulans*; Parrish 2008; D.R. Towns, unpublished data).

11.3 Lizards After European Contact

Despite the importance of lizards in Māori worldviews, early New Zealand governments were slow to protect lizards or any other native species. The first native species to receive protection was the tuatara (Rhynchocephalia, *Sphenodon punctatus*) in 1895, ironically, under the guise of a lizard in a New Zealand Gazette notice proclaiming "tuatara lizards protected under the Animals Protection Acts". A similarly worded notice in 1898 protected "tuatara lizards and their eggs" (Cree 2014). In a recent decision, the Waitangi Tribunal (2011) concluded that having committed to the Treaty of Waitangi in 1840, New Zealand governments were in fact obliged to protect all taonga (treasures) in such a way that Māori could exercise kaitiakitanga (guardianship) over them. These obligations include taonga associated with the natural world. However, the most comprehensive legislation protecting native species (Wildlife Act, 1953) specifically *excluded* geckos and skinks from protection (Miskelly 2014). Instead, lizards did not receive complete formal protection for 43 years after the passage of the Wildlife Act and over 150 years after signing the treaty. Legislation that might assist with conservation of tuatara and lizards clearly has not resulted from treaty obligations. Rather, the legislation has been in response to public pressure, particularly that of influential voices in the scientific community (reviews in Cree 2014; Miskelly 2014).

The nineteenth-century scientific community had little appreciation of the size or significance of the lizard fauna (Shea 2016); only 20 % of the currently recognised taxa were described by 1900 (Hitchmough et al. 2016b). This lack of appreciation is hardly surprising given that lizard diversity and abundance were already reduced on the mainland of New Zealand before the arrival of Europeans and the reluctance of Māori to view, handle or even discuss lizards (Cree 2014). Added to a lack of perceived need to protect the fauna was confusion over identity for many species (especially skinks). This confusion continued for some until late in the twentieth century (Hitchmough et al. 2016b). For example, the largest skink, chevron skink (*Oligosoma homalonotum*), and the nocturnal shoreline species, *O. suteri*, were both described by Boulenger in 1906. However, a mix-up over labels meant that fruitless searches for *O. homalonotum* were conducted in the type locality for *O. suteri* (Mokohinau Islands), and the former species was lost for about 70 years until its rediscovery on Great Barrier Island (Hardy 1977).

Without legislated protection, there was little institutional incentive to identify and mitigate threats to the fauna. This attitude began to change when the Wildlife Act was amended in 1981, with an Order in Council that protected most (but not all) of the lizard fauna. The exceptions were four species commonly held as pets and listed in the amendment as common skink (*Leiolopisma nigriplantare maccanni*), copper skink (*Cyclodina aenea*), common gecko (*Hoplodactylus maculatus*) and forest gecko (*H. granulatus*). All were subsequently found to be species complexes, including some taxa with restricted distributions (Hitchmough et al. 2016b; Chapple and Hitchmough 2016). Protection of the remaining species was not completed until a second amendment in 1996 (Miskelly 2014).

11.4 Agents of Decline

Central to conservation biology is the principle that population declines can only be reversed when the agent(s) of decline have been identified and resolved (Caughley 1994; Veltman 1996). Considerable effort in recent years has thus been devoted to understanding the distributional range of lizards, whether these ranges are stable or declining and, if in decline, whether agents of decline can be identified. Until well into the twentieth century, potential threats to the fauna were largely speculative. Even when the likely effects of introduced predators were identified, the results were treated with scepticism. For example, a chapter on mammals in the *Natural History of New Zealand* (Williams 1973) presented the first evidence that kiore might limit the distribution of invertebrates, tuatara, lizards and small seabirds (Gibb and Flux 1973). This proposition was based on a study revealing the inverse relationship between the abundance of kiore and lizards (Whitaker 1973). While acknowledging that the effects of these rats might need further consideration, the authors then observed that kiore were often considered native and questioned whether it was time for later introductions to be given similar recognition.

11.4.1 Wildlife Trafficking

Among potential threats to lizards, Robb (1973) viewed the most significant as over-collection and habitat interference and identified the need to protect the entire lizard fauna. However, the partial protection achieved in 1981 exacerbated the problem of over-collection when thousands of geckos (probably of an undescribed taxon) were exported annually on the grounds that they were unprotected (Miskelly 2014).

Possibly in response to the earlier gecko exports, New Zealand lizards became a desirable commodity for wildlife traffickers, even after total protection was extended to all lizards within New Zealand in 1996. In one notorious example, a German national was intercepted in 2010 before departure from Christchurch International Airport with 44 geckos and skinks hidden in underwear (Phillips 2010). Occasionally, New Zealand species were apparently exported in exchange for exotic species. One property raided by wildlife enforcement officers near Auckland housed illegally held native species and imported chameleons and geckos (D. Towns, unpublished data), a serious biosecurity risk (Chapple et al. 2016a). Although New Zealand laws prohibited interference and export, similar legislation did not necessarily apply to animals once they had been smuggled across the border. Illegal export is now covered by international conventions that regulate trade in endangered species. For example, New Zealand's diurnal green geckos are now on Schedule 2 of the Convention on International Trade in Endangered Species, which effectively means that possession without a permit is globally prohibited.

11.4.2 Invasive Species

The interception of traffickers at the border can generate considerable media interest (e.g. Phillips 2010; Bayer 2012), but the numbers involved in most cases are likely less than the daily intake of lizards by a single feral cat (*Felis catus*). The potential for introduced predators to influence the distribution and abundance of lizards became apparent by comparing the distributions of lizards and *Rattus exulans* within and between archipelagos (Whitaker 1973, 1978). The relict nature of many lizard distributions was subsequently supported by discoveries on the mainland of subfossil remains of species now confined to islands (Worthy 1987; Towns and Daugherty 1994; Worthy 2016). A telling indicator of the effects of predators in agricultural land on the mainland came from the stomach contents of feral cats. A cat killed mid-morning in rural Central Otago contained 15 skinks of three different species, including an endangered *Oligosoma grande* (Daugherty and Towns 1991). In urban Auckland, lizards were the third most common group identified as prey of domestic cats (Gillies and Clout 2003). Other introduced mammalian predators of lizards include three species of mustelids and four species of rodents, hedgehogs (*Erinaceus europaeus*), pigs (*Sus scrofa*) and possibly possums (*Trichosurus vulpecula*; King 2005). Furthermore, introduced mammals can operate as a guild, with complex changes in the impacts of each species as a result of any changes in the abundance of other species in the guild (Reardon et al. 2012; Norbury et al. 2013). The circumstantial evidence of lizard suppression by predators on islands, fragmentary evidence from cats on the mainland and recent confirmation of positive responses by lizard populations to intensive mammal control or removal in fenced sanctuaries on the mainland (see Sect. 11.6.2; Nelson et al. 2016) suggest pervasive effects by introduced species on virtually all native lizard species. Combined with habitat loss on the mainland, increasing clarity over the effects of invasive species has led to four crucial activities: development of threat classification systems, a process for identifying threats to individual species, research into the effects of invasive species including introduced reptiles (Nelson et al. 2014; Chapple et al. 2016a) and testing of methods to mitigate these threats. Each of these is covered in more detail below.

11.5 Threat Classification

The first threat lists of New Zealand lizards were released in 1981 and based almost totally on expert opinion, using International Union for the Conservation of Nature (IUCN) criteria. These lists lacked defensible criteria for inclusion and offered little guidance to ensure consistency across taxa (e.g. Williams and Given 1981). Today, all extant native species of plants and animals are regularly assessed using the New Zealand Threat Classification System (NZTCS), which has many similarities to the IUCN system. However, the NZTCS has categories and criteria modified to account for the small areas or populations naturally occurring in archipelagos, such as New Zealand (Townsend et al. 2008). The two systems can produce different outcomes. For example, the skink *Oligosoma fallai*, which is endemic to the Three Kings Islands, is listed by the IUCN as vulnerable and as naturally uncommon under the NZTCS (Hitchmough et al. 2016a). "Naturally uncommon" is not used by the IUCN, but is applied by the NZTCS to uncommon species that have not suffered reductions to their historic range or population size (i.e. species whose current rarity or restricted distributions are not attributable to the effects of human activity; Townsend et al. 2008).

The number of extant species of lizards assessed has now reached >100, but the proportion regarded as threatened has varied (Fig. 11.2) as more information is obtained on indeterminate or data-deficient species. Current assessments (Hitchmough et al. 2016a) identify 36 % of the lizard fauna as threatened [nationally critical (NC), endangered (NE) or vulnerable (NV)]. Of the 22 formally named species classified as threatened (Table 11.2), 64 % are endemic to the South Island and only 14 % to the North Island. The remainder are confined to offshore islands. The proportion of threatened South Island species increases further if unnamed taxa are added (Hitchmough et al. 2016a). The preponderance of threatened species in the South Island and over-representation of larger ground-dwelling species were

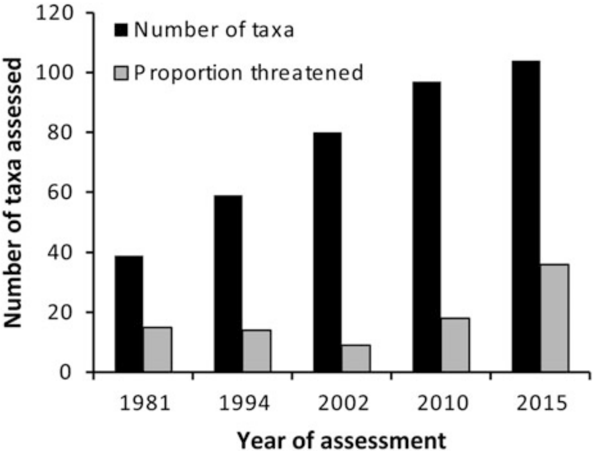


Fig. 11.2 Proportion of threatened species of New Zealand lizard relative to number of taxa assessed with data from Williams and Given (1981), Molloy et al. (1994), Hitchmough (2002) and Hitchmough et al. (2010, 2016a)

Table 11.2 Conservation status, habitat, threats and population trends of 37 species of New Zealand lizards currently listed as threatened (Hitchmough et al. 2016a)

Category and species	Habitat and location	Threats and trend	References
Nationally critical (NC)			
Oligosoma burganae	Above 900 m in tussockland and peat; Rock and Pillar and Lammermoor Ranges, Otago	Evidence of significant population declines, but likely causes unclear	Chapple et al. (2011)
O. tekakahu	Coastal herbfield and prostrate shrubs; Chalky Island, Fiordland National Park	Confined to small area on one island, but extensive potential habitat; island now free of mammalian predators	Chapple et al. (2011)
Nationally endangered (NE)			
Naultinus rudis	Scattered locations, eastern and central South Island	Shrub and other low vegetations, sometimes adjacent to beech (*Nothofagus* spp.) forest	Robb (1986) and Nielsen et al. (2011))
O. grande, *O. otagense*	Sympatric distribution in middle-altitude fractured schist in shrub and tussockland, Otago	Rapid declines of populations reversed with predator control at selected sites (see text)	Reardon et al. (2012) and Nelson et al. (2014)
O. judgei	High-altitude (>1100 m) alpine areas of cliffs and scree	Two of three populations within Fiordland National Park	Patterson and Bell (2009)
O. pikitanga	Middle-altitude (<1100 m) alpine and subalpine vegetated damp cliffs	Few specimens seen, but known range within Fiordland National Park	Bell and Patterson (2008)
O. taumakae	Confined to one group of small (<20 ha) low-lying offshore islands (Open Bay Islands)	Populations on main islands appear vulnerable to introduced weka (*Gallirallus australis*); islands under traditional ownership by Māori	Chapple and Patterson (2007) and Lettink et al. (2013)
O. whitakeri	Widely disjunct distribution, small islands off northeastern North Island to one coastal site, southern North Island	Appears vulnerable to introduced predators, near extinct on the mainland (see text)	Towns and Ferreira (2001), Hoare et al. (2007a) and Towns et al. (in press)
Nationally vulnerable (NV)			
Mokopirirakau cryptozoicus	Scattered locations in southwestern alpine South Island	All known sites are within Fiordland and Mt Aspiring National Parks and other conservation areas	Jewell and Leschen (2004) and Nielsen et al. (2011)
M. kahuturae	Seaward Kaikoura and Arthur Ranges, northern South Island	Strongly alpine, inhabits rock crevices above 1250 m, Arthur Range	Whitaker et al. (1999)

(continued)

Table 11.2 (continued)

Category and species	Habitat and location	Threats and trend	References
		population in Kahurangi National Park	
Naultinus stellatus	North-western South Island	Range from shrublands to beech (*Nothofagus*) forest; within Kahurangi, Nelson Lakes and Abel Tasman National Parks	Robb (1986) and Nielsen et al. (2011)
N. tuberculatus	Western South Island	Manuka (*Leptospermum*) and kanuka (*Kunzia* sp.) shrublands	Robb (1986) and Nielsen et al. (2011)
Toropuku stephensi	Maud and Stephens Islands, Cook Strait	Forested areas; both populations in strictly protected nature reserves	Robb (1986) and Nielsen et al. (2011)
Tukutuku rakiurae	Endemic to Stewart Island	Alpine shrub areas, within Rakiura National Park	Thomas (1981)
Oligosoma homalonotum	Hauturu/Little Barrier and Great Barrier Islands	Forested areas, often adjacent to streams or in debris dams; Hauturu is a strictly protected nature reserve (see text)	Neilson et al. (2006)
O. levidensum	Confined to the far northern North Island	Presumed forest litter	Chapple et al. (2008)
O. longipes	Foothills of northeastern Southern Alps	Dry rocky eroding river terraces and talus slopes	Patterson (1997) and Chapple et al. (2009)
O. microlepis	Scattered locations in central North Island and Motutaiko Island, Lake Taupo	Rock and bouldery areas; river beds, screes, outcrops and cliffs	Whitaker (1997), Towns et al. (2002) and Hitchmough et al. (2010)
O. repens	Eyre and Hector mountains of south Central Otago	Rock piles and screes around foothills	Chapple et al. (2011)
O. toka	Known from the Nevis Valley and Lindis Pass areas, south central South Island	Locally abundant around natural and artificial rock piles, including habitats modified by agriculture	Chapple et al. (2011)
O. waimatense	Eastern mountains and foothills associated with the Southern Alps, South Island	Eroding greywacke rocky scree but also other rock types, usually with little vegetation cover	Patterson (1997) and Chapple et al. (2012)

Fifteen species (41 %) without names have been excluded due to a lack of published data on distribution and habitat use

noted by Hitchmough et al. (2010), who also found an under-representation of threatened species on islands free of (introduced) predators. Subsequent modelling (Tingley et al. 2013) confirmed the role of body size as a predictor of threat status, as well as a potential role of habitat specialisation and range size. Examples of specialists include *Oligosoma tekakahu* (NC) confined to restricted habitats on one island and at least two species of skinks (NE) and two *Mokopirirakau* gecko species (NV) known only from restricted alpine habitats (Table 11.2; Chapple and Hitchmough 2016). The four species are all within national parks, where habitats are largely unmodified but potentially vulnerable to episodic irruptions of rodents and stoats (*Mustela erminea*). These irruptions are implicated in the range declines of other sympatric species, including rock wrens (*Xenicus gilviventris*; Michelsen-Heath and Gaze 2007). Other lizard species appear to be rocky habitat specialists, but their scattered distribution patterns may indicate secondary contraction to refugia due to habitat loss and predation at intervening sites. Examples include *O. microlepis* in the North Island and *O. longipes*, *O. repens*, *O. toka* and *O. waimatense* in the South Island (Table 11.2).

11.6 Threat Mitigation

11.6.1 Recovery Plans

Recovery plans were instigated for threatened species soon after the formation of the Department of Conservation in 1987, in order to coordinate activities and set agendas for improving conservation status (Nelson et al. 2014). Of the eight currently accepted lizard species that were identified within the "threatened" category (vulnerable or rare) in 1981, five were included in the earliest recovery plans. Our summary below focuses on these five since they have been involved in conservation actions for over 30 years and since one of us (DRT) has been part of a recovery team for all five species and a recovery plan author.

11.6.1.1 Robust (*Oligosoma alani*) and Whitaker's (*O. whitakeri*) Skinks

Robust and Whitaker's skinks are distinctive species; they are nocturnal, often most abundant in areas heavily burrowed by seabirds (Southey 1985; Hare et al. 2016), and largely incompatible with introduced predators. In addition, both species had undergone massive prehistoric range declines, with the two species by the early 1990s confined to two (Whitaker's skink) or three (robust skink) known sites (Towns 1992; Towns and Daugherty 1994). Adult robust skinks in the wild reach around 140-mm snout-vent length (SVL), whereas Whitaker's skinks are much smaller at 80–100-mm SVL (Towns 1999; Jewell 2008; Cree and Hare 2016). Nonetheless, recovery plans have dealt with both species together because they co-occur on some islands and occupy similar habitats (Chapple and Hitchmough 2016). Furthermore, for each species, Middle Island (13 ha) was the only site administered as conservation land. Early efforts for Whitaker's skink involved

Table 11.3 Conservation history of five species managed through recovery plans

Year, species, threat rank	Conservation actions to date	References
Oligosoma alani and *O. whitakeri*		
1981: *O. alani* rare, *O. whitakeri* vulnerable	Attempts to breed *O. alani* in captivity, none for *O. whitakeri*	Robb (1986) and Williams and Given (1981)
1994, 1996: both species category B for DOC (second highest priority), listed as vulnerable by the IUCN	Purchase of 12.3-ha Pukerua Bay habitat (1984), stock excluded (1987), gazetted as scientific reserve (1996); completion of the first recovery plan (1992); reintroduction to Korapuki Island of 28 *O. whitakeri* (1988) and 14 *O. alani* (1993); reintroduction of 30 of each species to Red Mercury Island (1994–1995) and 30 of each species to Kawhitu Island (1995)	Towns (1992), Molloy et al. (1994), Anonymous (1996), Baillie and Groombridge (1996) and Towns and Elliott (1996)
2002: both species range restricted	Reintroduction of 30 *O. alani* to Motuopao Island (1997), completion of the second recovery plan (1999), confirmation of successful establishment on Korapuki Island of *O. whitakeri* (2001)	Towns (1999), Towns and Ferreira (2001), Hitchmough (2002) and Sherley et al. (2010)
2010: *O. alani* at risk (recovering), *O. whitakeri* nationally endangered	Confirmation of successful establishment of *O. alani* on Korapuki Island (2008), completion of genetic studies of effects of reintroductions (2009)	Miller (2009), Hitchmough et al. (2010) and Towns et al. (in press)
2015: *O. alani* at risk (recovering), *O. whitakeri* nationally endangered	Success with captive breeding of *O. whitakeri* approaches sufficient numbers for release into the wild	Hitchmough et al. (2016a)
Oligosoma grande and *O. otagense*		
1981: *O. grande* vulnerable, *O. otagense* rare	Attempts to breed both species in captivity	Williams and Given (1981) and Robb (1986)
1994, 1996: both species category A for DOC (highest priority), listed as vulnerable by the IUCN	Extensive surveys of potential habitat completed (1988), completion of recovery plan (1995), purchase commenced of two locations with core habitat in middle-altitude native grass and shrubland	Molloy et al. (1994), Whitaker and Loh (1995) and Baillie and Groombridge (1996)
2002: both species nationally endangered	Indirect role of rabbits as drivers of lizard predation by	Hitchmough (2002) and Norbury (2001)

(continued)

Table 11.3 (continued)

Year, species, threat rank	Conservation actions to date	References
	introduced mammals demonstrated (2001)	
2010: both species nationally critical	Purchases of core habitat completed (ca 2004), effectiveness of cat suppression tested (2006), effectiveness of invasive mammal suppression and exclusion demonstrated (2012)	Tocher (2006), Hitchmough et al. (2010), Reardon et al. (2012) and Nelson et al. (2014)
2015: both species nationally endangered	Management success with predator control and captive rearing	Hitchmough et al. (2016a)
Oligosoma homalonotum		
1981: vulnerable	Attempts to breed in captivity	Williams and Given (1981) and Robb (1986)
1994, 1996: category A for DOC (highest priority), listed as vulnerable by the IUCN	Recovery plan completed (1993), second population discovered on Hauturu/Little Barrier Island (1993), further surveys of Hauturu/Little Barrier Island completed	Towns and McFadden (1993), Molloy et al. (1994) and Baillie and Groombridge (1996)
2002: nationally endangered	Revised recovery plan completed (2002), eradication of kiore from Hauturu/Little Barrier Island completed (2004), radiotelemetry study of habitat use completed (2006)	Hitchmough (2002), Towns et al. (2002) and Neilson et al. (2006)
2010: nationally vulnerable	Two private pest control initiatives underway on Great Barrier Island	Hitchmough et al. (2010)
2015: nationally vulnerable	Localised studies consistently indicate higher than expected densities on Great Barrier Island; increased frequency and range of sightings on Hauturu/Little Barrier Island	Hitchmough et al. (2016a)

Note that apparently inconsistent threat ranks are the result of changing threat classification systems and nomenclature

purchasing land at Pukerua Bay, the only mainland site occupied by the species (Table 11.3). However, the most viable long-term solution to the plight of both species was the removal of introduced predators, including rats, from islands in their former range. Systematic development of rat eradication technologies for islands began in 1986 (Towns and Broome 2003), and early successes were soon followed by reintroductions within the Mercury Islands archipelago, adjacent to Middle Island (Table 11.3). Scattered additional discoveries over intervening years increased the number of original sites for Whitaker's skinks to three (total <20 ha) and robust skinks to six (total ca 33 ha). Four populations of robust skinks, and three of Whitaker's skinks, have now been reintroduced to islands. In theory, the new populations also substantially increase the area occupied. However, although both species have met criteria for long-term persistence on Korapuki Island (Miller et al. 2014; Towns et al., in press), this is not the case at any of the other reintroduction sites. The robust skink is currently classified as at risk recovering (Hitchmough et al. 2016a), while Whitaker's skink is currently listed as "nationally endangered", largely due to the lack of management applied at Pukerua Bay (Table 11.2).

Faced with the need to manage a complex guild of introduced mammalian predators and rampant weeds at Pukerua Bay (Towns et al. 2001; Hoare et al. 2007a), conservation staff attempted predator and weed control. However, predator trapping and poisoning were not at levels sufficient to prevent the likely extinction of the sole mainland population (Hoare et al. 2007a). The only remaining option has been to capture the lizards, develop a population in captivity and later release them on islands within the region. Currently, about 50 Whitaker's skinks have resulted from the captive breeding programme (D. Keall pers. comm.), but a suitable site for their release has yet to be identified (L. Adams pers. comm.).

11.6.1.2 Grand (*Oligosoma grande*) and Otago (*O. otagense*) Skinks

The grand and Otago skinks are the two largest species within a diverse assemblage of skinks and geckos in middle-altitude native grass- and shrublands in the eastern South Island (Towns et al. 1985; Chapple and Hitchmough 2016). As in the previous example, the two species differ in size, with the grand skink smaller than the Otago skink (up to 115-mm and 130-mm SVL, respectively; Towns 1985; Cree and Hare 2016). However, unlike robust and Whitaker's skinks, grand and Otago skinks are diurnal and obligate basking species (Hare et al. 2016).

Considerable early effort in managing the two species was devoted to surveys of potential habitat, with the conclusion that all grand and Otago skink populations were affected by farming and none were on protected land (Table 11.3). The most productive habitats for both species were subsequently purchased, and these are now incorporated into the Redbank Scenic and Deighton Creek Nature Reserves (combined area of 2100 ha). After many decades of extensive pastoralism, which included periodic burning of native grasslands, native vegetation was replaced by exotic grasslands. Together with the continued intensification of agriculture, this change to vegetation cover was identified as a major concern for lizard survival (e.g. Whitaker 1996; Houghton and Linkhorn 2002). The effects on lizard numbers were further compounded by predation from introduced species such as cats (Tocher 2006), which was responsible, at least in part, for additional declines in both species, even in protected areas (Tocher 2006). However, despite intensive cat and ferret (*Mustela furo*) control, both skink species demonstrated continued declines in area of occupancy and abundance (Tocher 2006). Complex interactions between the introduced herbivore and predator guilds were demonstrated by Norbury (2001), who found that rabbit population dynamics indirectly drove pressure on lizards by cats and mustelids (particularly stoats, *Mustela erminea*, and ferrets) through their influence on predator numbers and behaviour. By extending the range of introduced predators to five species (including hedgehogs and mustelids) and comparing uncontrolled, extensively trapped and predator exclusion sites, Reardon et al. (2012) demonstrated rapid increases of the abundance of grand and Otago skinks in both treatment regimes. They concluded that extensive predator control could be a cost-effective method for reducing threats to these species (Nelson et al. 2014; Table 11.3). Indeed, although the status of the two species had been upgraded from nationally endangered in 2001 (Hitchmough 2002) to nationally critical in 2005 (Hitchmough et al. 2007), the recovering populations of both species in response to predator control prompted a shift back to nationally endangered in 2012 (Hitchmough et al. 2013).

11.6.1.3 Chevron Skink (*Oligosoma homalonotum*)

Despite being the largest skink in New Zealand (SVL >140 mm; Towns et al. 2002; Cree and Hare 2016), living populations of chevron skinks were only rediscovered on Great Barrier Island in the 1970s (Chapple and Hitchmough 2016). Intensive surveys of potential sites on the island began in 1982, with numerous sightings eventually collected across the island, many on conservation land (Towns et al. 2002). The species was subsequently discovered on Hauturu/Little Barrier Island (2817 ha), which is a nature reserve now free of introduced mammalian predators (Table 11.3). A damaged museum specimen from the Hokianga area of northern New Zealand, previously described as *O. gracilicorpus* (Hardy 1977), has also been attributed to this species (Chapple et al. 2009). These living and museum records indicate that chevron skinks inhabit forests and once had a distribution that encompassed the northern North Island and its largest offshore islands.

On Great Barrier Island, research using radio-tracking provided clues as to why so few individuals were encountered: lizards most commonly used areas within 13 m of streams and inhabited retreats in crevices and debris dams, as well as within trees. Arboreal retreats included large forest trees and the crowns of tree ferns and palms (Neilson et al. 2006). More recent surveys on Great Barrier Island (e.g. Barr 2009) indicate that the species may be locally more abundant than was previously thought. For example, J. Janssen (pers. comm.) caught over 70 individuals in 3 months in 2012. Whether an accidental introduction of the introduced plague skink (*Lampropholis delicata*) represents a threat to this or other lizard species on the Great Barrier Island is unclear (Chapple et al. 2016b). Several chevron skinks have also been seen on Hauturu/Little Barrier Island, where eradication of cats and *Rattus exulans* may enable the species to increase in abundance, but there have been no systematic surveys to test for recovery.

As a result of the detection of larger populations on Great Barrier Island and the potential for recovery on Little Barrier Island, the conservation status of chevron skinks has been downgraded from nationally endangered (Hitchmough 2002; Hitchmough et al. 2007) to nationally vulnerable (Hitchmough et al. 2010, 2016a).

11.6.2 Restoration of Islands and Virtual Islands

By 2013, invasive mammals had been eradicated from at least 104 islands (Towns et al. 2013), resulting in measured benefits for at least 7 gecko and 16 skink species through natural recovery or reintroductions (Bellingham et al. 2010). Successes with species recovery and ecological restoration projects on islands stimulated intensive pest control for insular areas on the mainland (Saunders 1990) in a bid to protect selected species or the whole ecosystems (Nelson et al. 2016). Furthermore, the initiative has been embraced by numerous community groups. By 2011, three or more invasive mammal species were being controlled in mainland restoration sites covering a total of 64,000 ha (Innes and Saunders 2011).

Invasive mammal control has produced measurable increases in the abundance of lizard species such as grand and Otago skinks (see above), and this likely applies to other lizard species with which they coexist. There are few other reports of lizards benefiting from intensive pest control at unfenced sites (Nelson et al. 2014), though some fenced protected areas have been or are being established; a 500-ha fenced peninsula at Shakespear Regional Park, near Auckland, has as its goal the enhancement of a particularly diverse lizard assemblage, while a drylands' fenced site under construction in the central South Island aims to restore lizard assemblages that has been pushed to extinction in the region (Butler et al. 2014).

With numerous islands now free of invasive mammals and a proliferation of virtual islands through fenced sites on the mainland (Nelson et al. 2016), appropriate restoration methods need to be developed. One essential component of restoration is translocation, which is defined as the intentional movement of species between locations (IUCN/SSC 2013). In a review of non-avian translocations in New Zealand, Sherley et al. (2010) identified 22 translocations of 13 gecko taxa and 46 translocations of 13 skink taxa. The translocations included salvages to remove animals from habitats earmarked to be destroyed (for developments, such as road building). Of the translocations identified by Sherley et al. (2010), 10 populations of 6 species of geckos and 24 populations of 12 species of skinks were the subject of introduction programmes as part of conservation projects on islands. Evidence of population expansion (as a basic measure of translocation success, stage 3 of Miller et al. 2014) is only available for six species (each as single population) on islands, including one population each of robust and Whitaker's skinks (see above, Towns et al., in press). The successful translocations of robust and Whitaker's skinks were the first for these species, therefore the one with the longest period available to allow establishment to reach the threshold of population expansion. For many other translocated populations of New Zealand lizards, the lack of observed population expansion may simply reflect the very slow intrinsic population increase rates and should not necessarily be interpreted to mean failure. For one species, Duvaucel's gecko (*Hoplodactylus duvaucelii*), population expansion was only evident 15 years after release (Bell and Herbert, in press).

11.7 Discussion

11.7.1 Immediate Threats to the Lizard Fauna

The threat classification systems currently used in New Zealand (NZTCS and IUCN) focus mainly on population size and trend, without necessarily attempting to understand agents of decline or how to reverse their effects. The Department of Conservation's prescriptions for ecosystem and species recovery attempt to fill those gaps (Anonymous 2016). Of necessity, such systems focus on immediate threats. Nonetheless, our list of threatened lizard species contains some species where agents of decline are ill defined or the extent of their effects unknown. Conservation planning becomes even more complicated if longer-term and more diffuse threats are included, but nonetheless they should be identified. Below, we summarise progress with resolving immediate threats for New Zealand lizards before discussing some of the more prominent longer-term issues.

In the context of immediate threats, 75 % of taxa have been classified into the broad categories of threatened (the sum of nationally critical, endangered or vulnerable) or at risk excluding species naturally uncommon. If naturally uncommon species are included, the proportion increases to 83 % (Hitchmough et al. 2016a). Despite recovery plans being in place for 25 years, four of the five species reviewed here remain within the threatened category. Only robust skinks have been downgraded to "at risk". The situation is not as bad as it seems; the number of threatened species has been inflated by a far greater understanding of the size and distribution of the New Zealand lizard fauna (Hitchmough et al. 2016b; Chapple and Hitchmough 2016). It is hardly surprising that new species discovered on the mainland will be those with relict or naturally restricted distributions (Hitchmough et al. 2016b). Furthermore, the NZTCS categories are of necessity broad, and population sizes often need to increase by nearly an order of magnitude for species to change category.

The recovery of lizard species that are particularly sensitive to introduced predators awaited a crucial advance: techniques for eliminating invasive rodents from islands. Labour-intensive ground-based mammal eradications provided some new sites for species such as robust and Whitaker's skinks, but it was the introduction of aerial spreading of rodenticide bait that allowed the number of potential islands for release to rapidly increase (Towns and Broome 2003; Towns et al. 2013). The outcome has been reintroduction of robust and Whitaker's skinks to several islands.

On the mainland, intensive efforts to protect grand and Otago skinks included a 5-year survey programme to determine the extent of remaining populations (e.g. Whitaker 1988). The data obtained from surveys then informed land purchases as reserves, in some cases involving negotiations over many years (D. Houston pers. comm.). Considerable research has also been conducted on the effects of agricultural intensification and the dynamics of the complex array of introduced mammals in middle-altitude grasslands. Armed with this knowledge, the efficiency of mammal control has greatly improved, with concurrent increases in the abundance of grand and Otago skinks (Reardon et al. 2012). As with the previous examples, time and patience are now required as the extent of recovery possible and optimal cost-efficiency of pest control are tested.

One particularly enigmatic species is the chevron skink. Low capture rates may have been attributed to the secretive habits of the species on Great Barrier Island, especially their use of arboreal retreats. However, capture rates increased substantially when G-minnow traps (fish funnel traps) were used instead of pitfall traps (B. Barr, J. Janssen pers. comm., Lettink and Hare 2016). With Hauturu/Little Barrier Island now free of all introduced mammals, there may be a response by resident chevron skinks. However, given the large size of the island, the lack of data on reproductive output (Cree and Hare 2016) and the wide range of forest habitats available for reptiles (e.g. Whitaker and Daugherty 1991), any increase in the abundance of these skinks may take many years to be measurable.

The most perplexing situation is that of the relict Whitaker's skink population on the mainland habitat at Pukerua Bay. This population is ca 700 km south of other surviving populations and therefore includes genetic variation not found elsewhere (Miller et al. 2009). Yet, a trade-off between the mainland population and populations on the islands was never identified as an option, either in recovery plans or in the conservation management strategy for the area (e.g. Anonymous 1996; Towns 1999). Despite the cost and effort of purchasing this area, conservation effort at the site has been minimal and, until recently, intermittent. The population is thus likely to disappear (Hoare et al. 2007a). In time, population increases of reintroduced populations may compensate, at least to some extent, for the losses at Pukerua Bay. This loss is reflected in the species' "nationally endangered" status (Hitchmough et al. 2016a).

11.7.2 Variations in Vulnerability to Threats

Evidence from mammal eradications on islands, predator control on the mainland and modelling of the roles of intrinsic and extrinsic variables supports suggestions that vulnerability to biotic disturbance varies within the lizard fauna (Towns and Daugherty 1994; Tingley et al. 2013). Species could thus be grouped by vulnerability to specific threats in order to identify appropriate conservation strategies (Table 11.4). For example, one group comprises night-active ground-dwelling skinks that appear sensitive to all invasive, mammalian predators and which have relict distributions, largely on islands. The test of this hypothesis is the successful reintroduction of these species to islands within their former range from which

Table 11.4 Likely agents of decline of New Zealand lizards

Agents of decline	Example species/assemblages	Evidence
Incompatibility with invasive predators	Robust (*Oligosoma alani*), McGregor's (*O. macgregori*), Whitaker's skink (*O. whitakeri*), *Oligosoma northlandi*	Subfossil remains on the mainland; secondary endemism on islands free of introduced mammals
Extreme vulnerability to invasive predators	Duvaucel's gecko (*Hoplodactylus duvaucelii*), moko skinks (*O. moco*), Suter's skinks (*O. suteri*)	Historic records on the mainland; secondary endemism on islands, coexist with some invasive predators; respond strongly to predator removal
High vulnerability to invasive predators and habitat loss	Otago (*O. otagense*) and grand skinks (*O. grande*)	Declines throughout the range with changes in agriculture, respond strongly to introduced mammal control
Vulnerability to invasive predators and habitat loss	Day-active geckos (*Naultinus*), forest geckos (*Mokopirirakau granulatus*), striped skink (*O. striatum*)	Persist in the presence of mammalian predators but at greatly reduced population density, respond to introduced mammal control
Vulnerability to habitat loss, but relatively tolerant of invasive predators via their use of habitat refugia	Skinks and geckos that inhabit rocky scree and cliffs	Declines where native vegetation cover or other habitats have been removed or modified
Vulnerability to intensive urban development, but relatively adaptable and will occupy urban areas	Copper skink (*O. aeneum*), ornate skink (*O. ornatum*), glossy brown skink (*O. zelandicum*)	Evidence of range declines in urban environments; also declines in natural habitat, but recovers in response to mammalian predator removal
Unclear causes or extent of historic declines	Chevron skink (*O. homalonotum*), alpine specialists	Extremely cryptic; often with narrow distribution, some showing secondary endemism

predators have been removed. For example, Duvaucel's geckos, *Woodworthia maculata*, and the skinks, *Oligosoma suteri* and *O. smithi*, appear to be sensitive to introduced predators and often become confined to refugia, but can respond rapidly through behavioural change and range expansion when invasive mammals are removed (e.g. Towns 2002; Towns et al. 2003; Hoare et al. 2007b; Monks et al. 2014). Other species, such as the grand and Otago skinks, appear able to tolerate some invasive mammals, but may be sensitive to the combined effects of predation and direct or indirect effects of habitat modification. The test of this hypothesis has been rapid changes in abundance when selected invasive predators are controlled, even in environments previously modified by farming.

Perhaps unsurprisingly, predator control and fenced, predator exclusion sites in forested regions of the North Island have produced fewer measurable responses from resident lizard species compared with those inhabiting South Island grasslands

(Nelson et al. 2014). Subfossil evidence indicates that many forest-dwelling species, once widespread on the North Island, are those species now confined to islands (Towns and Daugherty 1994; Worthy 2016); localised extinction rates have been particularly high in faunas once dominated by these large nocturnal species of skinks and geckos (see also Tingley et al. 2013). In the South Island, there are no records of nocturnal skinks, and carefully designed predator control appears to be more effective (Hare et al. 2016). As a consequence, recovery or restoration of lizard assemblages in many South Island environments might be possible with efficient pest control, without the need to completely eradicate invasive predators. However, restoration of lizard assemblages in parts of the North Island will likely require the establishment of predator exclusion areas and reintroductions from relict island populations.

Unlike the challenges on the North Island mainland, restoration of lizard assemblages on islands could enable fundamental shifts in the threat status of some species (Table 11.4). For example, in the Mercury Islands, robust and Whitaker's skinks, previously confined to a total area of 13 ha (Whitaker's skinks) or 16 ha (robust skinks), have been reintroduced to islands with a total area of 343 ha. With completion of other pest removal programmes, these species could occupy two additional islands within the group, bringing the total area available to the group to over 2000 ha. The total area could increase to around 4000 ha, if islands that are now available for introductions, and that have subfossil remains of these two species, are included in conservation efforts (Worthy 2016). With the addition of species that survived on islands in the presence of some invasive mammals, which has since been removed (the second category in Table 11.4), the entire assemblages of relict species are in the process of increasing in abundance and over large areas. An example is Hauturu/Little Barrier Island (2817 ha), where 13 species of lizards, including chevron and striped skinks (*Oligosoma striatum*), survived at low numbers or in confined areas. Since the removal of cats in 1980 and rats in 2004 (Bellingham et al. 2010), these suppressed populations of lizards now have an increased capacity to expand their ranges across the island.

11.7.3 Long-Term Challenges and Threats

Even if immediate conservation issues can be resolved, longer-term problems could compromise many successes. Potential problems include demographic and genetic challenges to relict and translocated populations, climate change and public perceptions and values. The long life spans and slow intrinsic growth rates of the most vulnerable species pose major challenges to their recovery and reintroduction (Hare et al. 2016; Cree and Hare 2016). Measuring the success of reintroductions can thus require decades of monitoring, thereby incurring considerable cost and long periods of uncertainty about the outcome. The processes of establishment have been clarified by Miller et al. (2014), who regarded a translocated population as viable when the number of individuals captured was greater than the number released, and the founders have largely been replaced in the breeding population by locally born individuals. For Whitaker's skinks, this measure can take over 20 years to achieve and will likely be longer for the larger robust skinks (Towns et al., in press; Cree and Hare 2016). Furthermore, the small source populations for translocations may be vulnerable to disturbance and the effects of reduced genetic heterozygosity (e.g. Jamieson 2015; Towns et al., in press). The combination of cryptic behaviour, low reproductive output and logistically challenging islands is likely reasons why the outcomes of only 24 % of reintroductions to islands have been assessed (Bellingham et al. 2010; Towns et al., in press).

The potential effects of climate change operate over even longer timescales, and the outcomes for lizards are uncertain (Sinervo et al. 2010; Nelson et al. 2014). The most vulnerable species are likely to be habitat specialists that might be forced out of available habitats. Alpine skinks and geckos may fall into this category, but risks for such species are unlikely to be assessed when the extent and nature of current habitats and threats remain unclear. Islands and other coastal areas will be affected by rising sea levels; however, all but the smallest islands are sufficiently rocky and precipitous to overcome likely detrimental effects of predicted rises (0.26–2.3 m), at least until the end of the twenty-first century (Courchamp et al. 2014). Lizards in coastal areas on the mainland are more likely to face problems due to the inundation of habitats already reduced in area by coastal development. Restoration on the largest islands should also ensure that thermal refuges are available as temperatures increase.

The most intractable long-term threats to the lizard fauna are socioecological: the enigmatic roles of values and economics. A harsh reality of all conservation work is the overriding influence of preferences (value judgements, e.g. Lawton 1997). These likely vary in different regions and across cultures. For example, to some Māori, constant reminders of the significance of lizards to their lives are carved onto marae and other structures. Similarly, Ngatiwai now proudly claim kaitiakitanga (guardianship) over chevron skinks, which they refer to as niho taniwha (Fig. 11.3). Elsewhere, inconsistencies generated by value judgements have generated unhelpful standoffs. For example, on the Open Bay Islands, the skink *Oligosoma taumakae* (Table 11.2), and an undescribed species of gecko (Hitchmough et al. 2010; Hitchmough et al. 2016b), appear threatened by an introduced population of subspecific hybrid weka (*Gallirallus australis*), a flightless rail. When conservation staff proposed to the Māori Trust administering the islands that the weka should be eradicated, the result was division within the trust and a social media campaign to save the weka (Anonymous 2010). Since the genetically compromised weka could not be relocated to the mainland, the only workable solution appeared to be a periodic harvest of weka. However, these harvests have yet to be conducted and their effectiveness yet to be tested, and the skinks remain endangered. This example raises three questions. First, was sufficient information about the issue provided to the members of the trust and the community at large? Second, does this example indicate that the community values a genetically compromised population of bird over a distinctive local species of lizard?

NIHO TANIWHA

Chevron Skink – Oligosoma Homalonotum

Niho taniwha ki a Ngātiwai

Niho taniwha is found in the Ngātiwai rohe, on Aotea (Great Barrier Island, also known as Piki Paria) and Hauturu (Little Barrier). These skinks are a very important taonga to Ngātiwai because they are endemic and unique to the Ngātiwai area. These skinks are called niho taniwha because of the triangle shapes on their back, representing the teeth of the taniwha.

Niho is associated with oratory, and when niho taniwha is used in oratory to describe a person's attributes, it represents courage in war. When the niho taniwha pattern is used in whakairo, it depicts a rangatira and his authority, as well as the chiefly lineage of people of that house.

Kawa marae at Aotea hopes to use the niho taniwha pattern for tukutuku and kōwhaiwhai patterns.

Ngātiwai feels honoured that this taonga lives in our rohe, and as kaitiaki we want to maintain the importance of this species. On Aotea, niho taniwha are found in bushes and in places where there have been rockfalls.

It is thought that one of the reasons why the niho taniwha has survived on Aotea and Hauturu is that there are measures in place to protect these islands from certain introduced predators. However, niho taniwha are found to be surviving in non-protected areas on Aotea.

How big?

Niho taniwha can grow to over 30cm from its nose to the tip of its tail, making it New Zealand's longest skink.

Where to find them

Some adults have been seen well away from streams over winter but most sightings during summer have been close to forested streams or other damp places.
Niho taniwha can be found in the Ngātiwai rohe on Aotea and occasionally on Hauturu.

Niho taniwha often grunt or "speak" when disturbed. They are secretive and have excellent camouflage. Females can give birth to as many as eight live young at once, usually in mid to late summer.

During heavy rain, niho taniwha have been seen to climb trees to avoid flooding.

Science

Some researchers believe that skinks arrived about 25–35 million years ago, when most of New Zealand was submerged.

First scientifically described in 1906, the niho taniwha (then called the Chevron Skink) had been "lost" from science for over 60 years. Incorrect museum labelling has been attributed with this loss, since it was found that the niho taniwha's locality was labelled the Mokohinau Islands group, instead of the correct location of Aotea.

Endangered?

The niho taniwha is one of New Zealand's rarest skinks. It is listed as "nationally vulnerable" under the Department of Conservation's Threat Classification System, with only 500 reported sightings since it was first described in 1906.

Menu

Niho taniwha eat small insects that they find under dead leaves and foliage.

Danger

Norway rats, pigs and domestic and feral cats can be a threat to niho taniwha. One domestic cat alone is known to have brought home at least six.

Despite there being little traffic on Aotea, several niho taniwha are run over on the island's roads each year.

Identifying a niho taniwha

Niho taniwha have distinctive v-shaped markings on their backs and a pale coloured "teardrop" shape can be seen between two dark bands extending down the face from below the eye to just under the lower lip. Each niho taniwha has its own unique pattern.

Department of Conservation
Te Ara www.teara.govt.nz
Ngātiwai whānau
Images: Ben Barr

www.ngatiwai.ac.nz

NGĀTIWAI
EDUCATION
Te Au Here o Tūkaiaia

Fig. 11.3 Poster produced by Ngatiwai advertising their role as kaitiaki of the chevron skink, niho taniwha, named in recognition of the tooth-like markings on the body (www.ngatiwai.iwi.nz). ©Copyright 2013 Ngātiwai Trust Board. All rights reserved. Website by maio.co.nz

Third, is it reasonable to expect the implementation of well-intentioned solutions if appropriate funds or infrastructure are not allocated to them?

Limited funding and conflict among social issues have led to the development of priority-setting models (e.g. Anonymous 2016), although these could lead to inefficiencies if funds are directed only to the rarest species (Joseph et al. 2009). Such conundrums can be resolved with multiagency alliances. One such alliance developed for conservation of tuatara involves a consortium consisting of the Department of Conservation (DOC), other research organisations, Māori tribes (iwi) and professional groups, such as the Society for Research on Amphibians and Reptiles in New Zealand (Cree 2014). A similar approach seems to be aiding conservation management of grand and Otago skinks, with community groups investing in fenced invasive mammal exclusion sites. For example, the Central Otago Ecological Trust (www.coet.org.nz; Nelson et al. 2016) is responsible for managing a fenced site for the protection of Otago skinks. Another model derives from statutory social contracts between the iwi and the Crown after ownership over five islands in the Hauraki Gulf Marine Park was settled in 2012 and 2015. The settlements require DOC and iwi to develop co-management arrangements for Hauturu/Little Barrier (New Zealand Government 2012), Rangitoto-Motutapu, Motuihe and Tiritiri Matangi Islands (New Zealand Government 2014), all of which have expanding reptile populations and considerable restoration potential following invasive mammal eradications (Bellingham et al. 2010).

Elsewhere, the long-term social and economic threats facing lizards might best be approached through the use of modern socioecological analytical tools to understand public attitudes to lizards (e.g. Schultz 2011). If we know how the public at key locations view the New Zealand lizard fauna, appropriate messages about the diversity and significance of the fauna can be provided. It will then be possible to define the role these communities can play in their conservation. Socioecological approaches to conservation issues have so far rarely been applied anywhere, but may provide the only lasting solutions to the long-term threats facing New Zealand lizards.

Acknowledgements We thank Pare Keiha and Hare Paniora for their advice with the sections of this account that relate to Māori, Nicky Nelson for her useful review of the text and the Ngatiwai Trust Board for the permission to incorporate their poster of niho taniwha. We acknowledge the late Matua John Marsh for his support and tuition of one of us (JP) in Ngati Whakaue-Te Arawatanga. E Matua, nau i whatu te kakahu, he taniko taku (yours is the useful work, mine ornamental).

References

Anderson A, Binney J, Harris A (2014) Tangata whenua. Bridget Williams Books, Thorndon

Anonymous (1996) Conservation management strategy for Wellington 1996–2005. Department of Conservation, Wellington

Anonymous (2010) DOC may kill weka to save other natives. Otago Daily Times, 20 Feb

Anonymous (2016) Identifying conservation priorities. http://www.doc.govt.nz/about-us/our-role/managing-conservation/natural-heritage-management/identifying-conservation-priorities. Accessed 29 Jan 2016

Baillie J, Groombridge B (1996) Red list of threatened animals. IUCN, Gland and Cambridge

Barr BP (2009) Spatial ecology, habitat use, and the impacts of rats on chevron skinks (*Oligosoma homalonotum*) on Great Barrier Island. MSc thesis, Massey University, Auckland

Bayer K (2012) German poacher jailed for gecko smuggling. NZ Herald, 4 May

Bell T, Herbert S (in press) Establishment of a self-sustaining population of a long-lived, slow-breeding gecko (Diplodactylidae: *Hoplodactylus duvaucelii*) evident 15 years after translocation. J Herpetol

Bell TP, Patterson GB (2008) A rare alpine skink *Oligosoma pikitanga* n. sp. (Reptilia: Scincidae) from Llawrenny Peaks, Fiordland, New Zealand. Zootaxa 1882:57–68

Bellingham PJ, Towns DR, Cameron EK, Davis JJ, Wardle DA, Wilmshurst JM, Mulder CPH (2010) New Zealand island restoration: seabirds, predators, and the importance of history. N Z J Ecol 34:115–136

Best E (2015) Maori religion and mythology, part II. New Zealand electronic text collection, Victoria University of Wellington

Binney J (1995) Redemption songs a life of Te Kooti Arikirangi te Turuki. Auckland University Press with Bridget Williams Books, Auckland

Butler D, Lindsay T, Hunt J (2014) Paradise saved. Random House, Auckland

Caughley G (1994) Directions in conservation biology. J Anim Ecol 63:215–244

Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Patterson GB (2007) A new skink species (*Oligosoma taumakae* sp. nov.; Reptilia: Scincidae) from the Open Bay Islands, New Zealand. N Z J Zool 34:347–357

Chapple DG, Patterson GB, Bell T, Daugherty CH (2008) Taxonomic revision of the New Zealand copper skink (*Cyclodina aenea*: Squamata: Scincidae) species complex, with descriptions of two new species. J Herpetol 42:437–452

Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). Mol Phylogenet Evol 52:470–487

Chapple DG, Bell TP, Chapple SNJ, Miller KA, Daugherty CH, Patterson GB (2011) Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma inconspicuum*; Reptilia: Scincidae) species complex. Zootaxa 2782:1–33

Chapple DG, Birkett A, Miller KA, Daugherty CH, Gleeson DM (2012) Phylogeography of the endangered Otago skink, Oligosoma otagense: population structure, hybridisation and genetic diversity in captive populations. PLoS One 7(4):e34599. doi:10.371/journal.pone.0034599

Chapple DG, Knegtmans J, Kikillus H, van Winkel D (2016a) Biosecurity of exotic reptiles and amphibians in New Zealand: building upon Tony Whitaker's legacy. J R Soc N Z 46:66–84

Chapple DG, Reardon JT, Peace JE (2016b) Origin, spread and biology of the invasive plague skink (*Lampropholis delicata*) in New Zealand. Chap. 13. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Courchamp F, Hoffmann BD, Russell JC, Leclerc C, Bellard C (2014) Climate change, sea-level rise, and conservation: keeping island biodiversity afloat. Trends Ecol Evol 29:127–130

Cree A (2014) Tuatara Biology and conservation of a venerable survivor. Canterbury University Press, Christchurch

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Daugherty CH, Towns DR (1991) The cat's breakfast. N Z Sci Mon (April 1991):13–14

Daugherty CH, Towns DR, Atkinson IAE, Gibbs GW (1990) The significance of the biological resources of New Zealand islands for ecological restoration. In: Towns DR, Daugherty CH, Atkinson IAE (eds) Ecological restoration of New Zealand Islands, Conservation sciences publication no. 2. Department of Conservation, Wellington, pp 9–21

Gibb JA, Flux JEC (1973) Mammals. In: Williams GR (ed) The natural history of New Zealand. AH and AW Reed, Wellington, pp 334–371

Gillies C, Clout M (2003) The prey of domestic cats (*Felis catus*) in two suburbs of Auckland city, New Zealand. J Zool 259:309–315

Haami B (2013) Ngārara—reptiles—what are ngārara? Te Ara—the Encyclopedia of New Zealand. www.TeAra.govt.nz/

Hardy GS (1977) The New Zealand Scincidae (Reptilia: Lacertilia); a taxonomic and zoogeographic study. N Z J Zool 4:221–325

Hare KM, Chapple DG, Towns DR, van Winkel D (2016) The ecology of New Zealand's lizards. Chap. 6. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hickson RE, Slack KE, Lockhart P (2000) Phylogeny recapitulates geography, or why New Zealand has so many species of skinks. Biol J Linn Soc 70:415–433

Hitchmough R (compiler) (2002) New Zealand threat classification system lists. Department of Conservation, Wellington

Hitchmough RA, Hoare JM, Jamieson H, Newman D, Tocher MD, Anderson PJ, Lettink M, Whitaker AH (2010) Conservation status of New Zealand reptiles, 2009. N Z J Zool 37:203–224

Hitchmough R, Barr B, Lettink M, Monks J, Reardon J, Tocher M, van Winkel D, Rolfe J (2016a) Conservation status of New Zealand reptiles, 2015. Department of Conservation, Wellington

Hitchmough R, Bull L, Cromarty P (Compilers) (2007) New Zealand threat classification system lists 2005. Department of Conservation, Wellington

Hitchmough R, Anderson P, Barr B, Monks J, Lettink M, Reardon J, Tocher M, Whitaker T (2013) Conservation status of New Zealand reptiles, 2012. Department of Conservation, Wellington

Hitchmough RA, Patterson GB, Chapple DG (2016b) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hoare JM, Adams LK, Bull LS, Towns DR (2007a) Attempting to manage complex predator-prey interactions fails to avert imminent extinction of a threatened New Zealand skink population. J Wildl Manage 71:1576–1584

Hoare JM, Pledger S, Nelson NJ, Daugherty CH (2007b) Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. Biol Conserv 136:510–519

Houghton C, Linkhorn R (2002) Population decline in the skinks *Oligosoma otagense* and *O. grande* at Macraes Flat, Otago, DOC science internal series 32. Department of Conservation, Wellington

Innes J, Saunders A (2011) Eradicating multiple pests: an overview. In: Veitch CR, Clout MN, Towns DR (eds) Island invasives: eradication and management. IUCN, Gland, pp 177–181

IUCN/SSC (2013) Guidelines for reintroductions and other conservation translocations. Version 1.0., Gland

Jamieson IG (2015) Significance of population genetics for managing small natural and reintroduced populations in New Zealand. N Z J Ecol 39:1–18

Jewell T (2008) A photographic guide to reptiles and amphibians of New Zealand. New Holland, Auckland

Jewell TR, Leschen RB (2004) A new species of *Hoplodactylus* (Reptilia: Pygopodidae) from the Takitimu Mountains, South Island, New Zealand. Zootaxa 792:1–11

Joseph LN, Maloney RF, Possingham HP (2009) Optimal allocation of resources among threatened species: a project prioritization protocol. Conserv Biol 23:328–338

King CM (ed) (2005) The handbook of New Zealand mammals. Oxford University Press, Melbourne, VIC

Lawton JH (1997) The science and non-science of conservation biology. N Z J Ecol 21:117–120

Lettink M, Hare KM (2016) Sampling techniques for New Zealand lizards. Chap. 10. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Lettink M, Hopkins G, Wilson RL (2013) A significant range extension and sanctuary for the rare Open Bay Island skink (*Oligosoma taumakae*). N Z J Zool 40:160–165

Michelsen-Heath S, Gaze P (2007) Changes in abundance and distribution of the rock wren (*Xenicus gilviventris*) in the South Island, New Zealand. Notornis 54:71–78

Miller KA (2009) Founding events and the maintenance of genetic diversity in reintroduced populations. PhD thesis, Victoria University, Wellington

Miller KA, Chapple DG, Towns DR, Ritchie PA, Nelson NJ (2009) Assessing genetic diversity for conservation management: a case study of a threatened reptile. Anim Conserv 12:163–171

Miller KA, Bell TP, Germano JM (2014) Understanding publication bias in reintroduction biology: an assessment of translocations of New Zealand's herpetofauna. Conserv Biol 28:1045–1056

Miskelly CM (2014) Legal protection of New Zealand's indigenous terrestrial fauna—an historical review. Tuhinga 25:25–101

Molloy J, Davis A, Tisdall C (1994) Setting priorities for the conservation of New Zealand's threatened plants and animals, 2nd edn. Department of Conservation, Wellington

Monks JM, Monks A, Towns DR (2014) Correlated recovery of five lizard populations following eradication of invasive mammals. Biol Invasions 16:167–175

Moorfield JC (2011) Te Aka Māori—English, English—Māori dictionary. Longman/Pearson Education, Auckland

Neilson K, Curran JM, Towns DR, Jamieson H (2006) Habitat use by chevron skinks (*Oligosoma homalonotum*) (Sauria: Scincidae) on Great Barrier Island, New Zealand. N Z J Ecol 30:345–353

Nelson NJ, Hitchmough R, Monks JM (2014) New Zealand reptiles and their conservation. In: Stow A, Maclean N, Holwell GI (eds) Austral Ark: the state of wildlife in Australia and New Zealand. Cambridge University Press, Cambridge, pp 382–404

Nelson NJ, Romijn RL, Dumont T, Reardon JT, Monks JM, Hitchmough RA, Empson R, Briskie JV (2016) Lizard conservation in mainland sanctuaries. Chap. 12. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

New Zealand Government (2012) Ngāti Manuhiri Claims Settlement Act, 2012. www.legislation.govt.nz

New Zealand Government (2014) Ngā mana whenua o Tāmaki Makaurau Collective Redress Act, 2014. www.legislation.govt.nz

Nielsen SV, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol 59:1–22

Norbury G (2001) Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. J Appl Ecol 38:1350–1361

Norbury G, Byrom A, Pech R, Smith J, Clarke D, Anderson D, Forrester G (2013) Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. Ecol Appl 23:1707–1721

Parrish R (2008) Re-introduction of skink and gecko species to Marotere Islands, Northland, New Zealand. In: Soorae PS (ed) Global re-introduction perspectives. IUCN/SSC Reintroduction Specialist Group, Environment Agency Abu Dhabi and Denver Zoological Foundation, Abu Dhabi, pp 62–65

Patterson GB (1997) South Island skinks of the genus *Oligosoma:* description of *O. longipes* n. sp. with redescription of *O. otagense* (McCann) and *O. waimatense* (McCann). J R Soc N Z 27:439–450

Patterson GB, Bell TP (2009) The Barrier skink *Oligosoma judgei* n. sp. (Reptilia: Scincidae) from the Darran and Takitimu Mountains, South Island, New Zealand. Zootaxa 2271:43–56

Phillips T (2010) Man smuggled 44 lizards in his underpants. Metro 27 Jan (www.metro.co.uk)

Reardon JT, Whitmore N, Holmes KM, Judd LM, Hutcheon AD, Norbury G, Mackenzie DI (2012) Predator control allows critically endangered lizards to recover on mainland New Zealand. N Z J Ecol 36:141–150

Robb J (1973) Reptiles and Amphibia. In: Williams GR (ed) The natural history of New Zealand. AH and AW Reed, Wellington, pp 285–303

Robb J (1986) New Zealand amphibians and reptiles in colour. Collins, Auckland

Saunders A (1990) Mapara: island management “mainland” style. In: Towns DR, Daugherty CH, Atkinson IAE (eds) Ecological restoration of New Zealand islands. Department of Conservation, Wellington, pp 147–149

Schultz PW (2011) Conservation means behaviour. Conserv Biol 25:1080–1083

Shea GM (2016) History of discovery of the New Zealand lizard fauna. Chap. 2. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Sherley GH, Stringer IAN, Parrish GR (2010) Summary of native bat, reptile, amphibian and terrestrial invertebrate translocations in New Zealand, Science for conservation 303. Department of Conservation, Wellington

Sinervo B, Mendez-De la Cruz F, Miles DB, Heulin B, Bastiaans E, Santa Cruz MV, Lara-Resendiz R, Martinez-Méndez N, Calderon-Espinosa ML, Mesa-Lázaro RN, Gadsden H, Avila LJ, Morando M, De la Riva IJ, Sepulveda PV, Rocha CFD, Ibargüengoytia N, Puntriano CA, Massot M, Lepetz V, Oksanen TA, Chapple DG, Bauer AM, Branch WR, Clobert J, Sites JW (2010) Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–899

Southey IC (1985) The ecology of three rare skinks on Middle Island, Mercury Islands. MSc thesis, University of Auckland, Auckland

Stone RCJ (2001) From Tamaki Makau-rau to Auckland. Auckland University Press, Auckland

Tennyson A, Martinson P (2006) Extinct birds of New Zealand. Te Papa Press, Wellington

Thomas BW (1981) Hoplodactylus rakiurae n. sp. (Reptilia: Gekkonidae) from Stewart Island, New Zealand, and comments on the taxonomic status of Heteropholis nebulosus McCann. N Z J Zool 8:33–47

Tingley R, Hitchmough RA, Chapple DG (2013) Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol Conserv 165:62–68

Tocher MD (2006) Survival of grand and Otago skinks following predator control. J Wildl Manage 70:31–42

Towns DR (1985) The status and prospects of the rare New Zealand lizards *Leiolopisma grande* (Gray), *Cyclodina whitakeri* Hardy and *Leiolopisma otagense* McCann (Lacertilia: Scincidae). In: Shine R, Ehmann H, Grigg G (eds) Biology of Australasian frogs and reptiles. Royal Society of New South Wales, Chipping Norton, NSW, pp 481–489

Towns DR (1992) Recovery plan for Whitaker’s and robust skink, Threatened species unit recovery plan series no. 3. Department of Conservation, Wellington

Towns DR (1999) *Cyclodina* spp. recovery plan, Threatened species recovery plan series 27. Department of Conservation, Wellington

Towns DR (2002) Interactions between geckos, honeydew scale insects and host plants revealed on islands in northern New Zealand, following eradication of introduced rats and rabbits. In: Veitch CR, Clout MN (eds) Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group, Gland and Cambridge, pp 329–335

Towns DR, Broome KG (2003) From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. N Z J Zool 30:377–398

Towns DR, Daugherty CH (1994) Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonization. N Z J Zool 21:325–339

Towns DR, Elliott GP (1996) Effects of habitat structure on distribution and abundance of lizards at Pukerua Bay, Wellington, New Zealand. N Z J Ecol 20:191–206

Towns DR, Ferreira SM (2001) Conservation of New Zealand lizards (Lacertilia: Scincidae) by translocation of small populations. Biol Conserv 98:211–222

Towns DR, McFadden I (1993) Chevron skink recovery plan Leiolopisma homalonotum. Department of Conservation, Wellington

Towns DR, Daugherty CH, Newman DG (1985) An overview of the ecological biogeography of the New Zealand lizards (Gekkonidae, Scincidae). In: Shine R, Ehmann H, Grigg G (eds) Biology of Australasian frogs and reptiles. Royal Society of New South Wales, Chipping Norton, NSW, pp 107–115

Towns DR, Daugherty CH, Cree A (2001) Raising the prospects for a forgotten fauna: a review of 10 years of conservation effort for New Zealand reptiles. Biol Conserv 99:3–16

Towns DR, Neilson KA, Whitaker AH (2002) North Island Oligosoma spp. skink recovery plan 2002–2012, Threatened species recovery plan 48. Department of Conservation, Wellington, 60p

Towns DR, Parrish GR, Westbrooke I (2003) Inferring vulnerability to introduced predators without experimental demonstration: case study of Suter's skink in New Zealand. Conserv Biol 17:1361–1371

Towns DR, West CK, Broome KG (2013) Purposes, outcomes and challenges of eradicating invasive mammals from New Zealand islands: an historical perspective. Wildl Res 40:94–107

Townsend AJ, de Lange PJ, Duffy CAJ, Miskelly CM, Molloy J, Norton D (2008) New Zealand threat classification system manual. Department of Conservation, Wellington

Veltman CJ (1996) Investigating causes of population decline in New Zealand plants and animals: introduction to symposium. N Z J Ecol 20:1–5

Westervelt WD (1910) Legends of Ma-ui – a demigod of Polynesia, and of his mother Hina. Hawaiian Gazette

Whitaker AH (1973) Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). Proc N Z Ecol Soc 20:121–130

Whitaker AH (1978) The effects of rodents on reptiles and amphibians. In: Atkinson IAE, Dingwall PR, Hay C (eds) The ecology and control of rodents in New Zealand nature reserves, Information series 4. New Zealand Department of Lands and Survey, Wellington, pp 75–88

Whitaker AH (1988) A survey of the lizards of the Rock and Pillar Range area, Otago 8−17 Mar 1988. Unpublished report, Department of Conservation, Dunedin

Whitaker AH (1996) Impact of agricultural development on grand skink (*Oligosoma grande*) (Reptilia: Scincidae) populations at Macraes Flat, Otago, New Zealand, Science for conservation 33. Department of Conservation, New Zealand

Whitaker AH (1997) Small-scaled skinks (*Oligosoma microlepis*) in the east Taupo region, central North Island. Unpublished report, Department of Conservation, Wanganui

Whitaker AH, Daugherty CH (1991) Research on the tuatara (*Sphenodon punctatus*) of Little Barrier Island, 5−12 Feb 1991. Unpublished report, Department of Conservation, Wellington

Whitaker AH, Loh G (1995) Otago skink and grand skink recovery plan (*Leiolopisma otagense and L. grande*). Department of Conservation, Wellington

Whitaker A, Shaw T, Hitchmough R (1999) Black-eyed geckos *(Hoplodactylus kahutarae)* on Mt Arthur, Kahurangi National Park. Department of Conservation, Wellington

Williams GR (ed) (1973) The natural history of New Zealand. AH and AW Reed, Wellington

Williams GR, Given DR (1981) The red data book of New Zealand. Nature Conservation Council, Wellington

Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH (2008) Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. PNAS 105:7676–7680

Worthy TH (1987) Osteological observations on the larger species of the skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. N Z J Zool 14:219–229

Worthy TH (2016) A review of the fossil record of New Zealand lizards. Chap. 3. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapter 12
Lizard Conservation in Mainland Sanctuaries

Nicola J. Nelson, Richard L. Romijn, Terra Dumont, James T. Reardon, Joanne M. Monks, Rodney A. Hitchmough, Raewyn Empson, and James V. Briskie

Abstract Mainland sanctuaries, where introduced mammalian predators are controlled or excluded, have the potential to improve the conservation status of New Zealand lizards. This is due to the reliance of a large number of species on habitats unavailable on offshore islands. However, despite considerable predator control efforts, lizard populations are still in decline, even in some mainland sanctuaries. The main cause of this failure appears to be that predator control is hard to sustain and largely targeted at protecting bird populations, which require

---

N.J. Nelson (✉) • R.L. Romijn
Victoria University of Wellington, PO Box 600, Wellington, New Zealand
e-mail: nicola.nelson@vuw.ac.nz; richardromijnnz@gmail.com

T. Dumont
Department of Conservation—Te Papa Atawhai, Kā Moana Haehae/Alexandra Office,
43 Dunstan Rd, PO Box 76, Alexandra 9340, New Zealand
e-mail: terra.dumont@gmail.com

J.T. Reardon
Department of Conservation—Te Papa Atawhai, Fiordland District Office, PO Box 29m,
Te Anau 9400, New Zealand
e-mail: jreardon@doc.govt.nz

J.M. Monks
Department of Conservation, PO Box 5244, Dunedin 9058, New Zealand
e-mail: jmonks@doc.govt.nz

R.A. Hitchmough
Department of Conservation—Te Papa Atawhai, National Office, PO Box 10 420, Wellington,
New Zealand
e-mail: rhitchmough@doc.govt.nz

R. Empson
ZEALANDIA, 53 Waiapu Road, Karori, Wellington, New Zealand
e-mail: Raewyn.Empson@visitzealandia.com

J.V. Briskie
School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch,
New Zealand
e-mail: jim.briskie@canterbury.ac.nz

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_12

lower levels of predator suppression than lizard populations. Even fenced, mainland, predator-exclusion sites are prone to reinvasions, particularly of mice, which are difficult to exclude at the outset. Episodic irruptions of mice within fenced sanctuaries, and other mammalian predator species in unfenced sanctuaries, can quickly decrease lizard numbers. Small lizard populations are particularly vulnerable. We discuss two case studies to illustrate population dynamics and limitations to understanding mechanisms underlying patterns of population declines in New Zealand skinks: ornate skinks (*Oligosoma ornatum*) in a fenced mainland site and speckled skinks (*O. infrapunctatum*) in an unfenced mainland site. We also speculate about the effects on lizards of native and non-native birds and introduced social insects, including wasps and ants. Understanding biological interactions and obtaining more species- and situation-specific data for lizards will provide information on limits to recovery, detection time frames after management actions, risks and benefits of habitat enhancements and density targets for introduced species where total eradication is impractical.

Keywords Conservation • Gecko • Invasive species • Mainland sanctuary • Ornate skink • Predation • Speckled skink

12.1 Introduction

The conservation of New Zealand's 100+ species of native lizards is reliant on the control or elimination of introduced mammals (Hitchmough et al. 2016a, b). In particular, this applies to rodents, mustelids and cats, which are known to both prey upon lizards directly and to compete with them for resources (Towns et al. 2001; Innes et al. 2010; Towns et al. 2016a). On offshore islands, it is often possible to eradicate the entire suite of introduced mammals, which usually allows native lizards to recover or be restored via translocations (Towns and Broome 2003; Towns et al. 2016a). However, islands represent only a small proportion of suitable habitats for lizards, and therefore conservation on the mainland is crucial for maintaining the full diversity of New Zealand lizards and restoring viable populations (Nelson et al. 2015).

Mainland sanctuaries are areas of protected native habitats that mimic islands in many aspects; they are surrounded by fences designed to exclude introduced mammals or threaded with a network of predator traps or poisoning arrays, which protect both their core areas from introduced predators and their boundaries from reinvasion (Saunders 2000). By the end of 2009, 8,396 ha, spanning 28 conservation areas, had been enclosed by 113 km of pest-proof fences and cleared of most mammalian pests (Burns et al. 2012). In addition, by 2011, a larger area (64,000 ha) was managed in unfenced mainland sanctuaries where at least three species of animal pest were controlled. This is an area even greater than the ~37,000 ha of pest-free habitat on offshore islands around the New Zealand coast (Innes and Saunders 2011).

Unfortunately, in predator control operations on the mainland, it is not always possible to eradicate all introduced mammals, even in fully fenced sanctuaries. Not only do these predators and/or competitors remain or reinvade the protected area (fenced or unfenced), but their potential effect might vary from year to year (e.g. Long et al. 2014). Indeed, some invasive mammal species are released from predation or competitor pressure by the removal of other mammalian pests through meso-predator (Crooks and Soulé 1999) or competitor release (Caut et al. 2007; Norbury et al. 2013). For example, mice (*Mus musculus*) experience competitor and predator release from rats (*Rattus* spp.), so if rats are removed, mice can reach plague numbers or reinvade sanctuaries. In Tāwharanui Open Sanctuary (Auckland), an area in which rats, but not mice, were effectively controlled, mice attained the highest densities (190 per 100 trap nights) ever recorded in New Zealand (Goldwater et al. 2012). Mice prey on lizards, and several studies have concluded that predation by mice can limit New Zealand lizard populations (Newman 1994; Hoare et al. 2007a; Wedding 2007; Norbury et al. 2013, 2014). At two coastal pebble beaches in the Tāwharanui Regional Park, shore skink (*Oligosoma smithi*) populations increased following the elimination of all introduced mammals, but when mice reinvaded and their populations irrupted, skink numbers declined (Graham Ussher, pers. comm.).

Conservationists are aware of these issues and often aim to eradicate all introduced mammalian predators and competitors, control subsequent incursions and manage pest population numbers via targeted poisoning or trapping operations. The success of predator control in a sanctuary is often demonstrated by subsequent growth of bird populations (Brown et al. 2015). However, birds vary in their sensitivity to different species and/or abundance of predatory mammals, and little is known about the thresholds for acceptable levels of pest mammals, especially mice. This is the case even for relatively well-studied bird populations (e.g. Long et al. 2014; Brown et al. 2015; Norbury et al. 2015). Empirical data on the level of predator control required for recovery of lizard populations in New Zealand are even more limited; there is insufficient data to assign a threat status to approximately 5 % of lizard species (Hitchmough et al. 2016a). Even for those species whose population sizes and trends are better known, understanding of the relationships between their population dynamics and specific mammalian predation pressure is lacking.

Quantifying the responses of indigenous biota of all types, including lizards, to conservation management is often hindered by limited resources, inadequate monitoring techniques and the complexity of their ecological interactions (reviewed in Norbury et al. 2015). On islands where mammalian pests have been eradicated, increases in the populations of endemic lizards demonstrate that the recovery of remnant populations is possible, although in some cases, these lizard populations grew from previously undetected source populations, highlighting the difficulty in monitoring small and cryptic species of reptiles at low densities (e.g. Hoare et al. 2007b). In addition, the time taken for recovery is likely determined by the life history characteristics of the species, as well as the size of the remnant population. For example, population growth estimates of translocated reptiles demonstrate that it will take decades to confirm success, because reproductive output can be as low as 7 % per annum for some species (e.g. Whitaker's skink, *O. whitakeri*; Towns and Ferreira 2001). Recent studies on the mainland also demonstrate that lizard populations can respond positively to control of mammalian predators (e.g. Reardon et al. 2012; Jones et al. 2013; Norbury et al. 2013). However, whether lizard populations are able to recover with low levels, or occasional incursions, of predatory mammals in mainland sanctuaries is likely to be species specific due to life history characteristics and behaviours and the size of the lizard population.

In general terms, over half the studies that examined the response of native New Zealand species (both plants and animals) to predator control demonstrated that unless pest densities were reduced below a key threshold level (which varied across species), populations did not recover (Norbury et al. 2015). Repeated incursions of predatory mammals into a sanctuary are likely to maintain lizard populations at low levels or create new bottlenecks. This, in turn, increases their vulnerability to stochastic events and to Allee and genetic effects related to small population sizes, such as reduced diversity and inbreeding (e.g. Towns and Ferreira 2001; Miller et al. 2009). Species with a low reproductive output and that are large-bodied, nocturnal and terrestrial are the least likely to be robust to fluctuations in mammal numbers. Indeed, these are over-represented in the extinction record (Towns and Daugherty 1994; Tingley et al. 2013).

At present, conservation in mainland sanctuaries predominantly targets birds, but where attention is given to reptiles, the typical goal is to support the recovery of existing resident species and then restore locally extinct lizard populations. The strength of mainland sanctuaries is that they have the potential to provide habitat not available on islands, and they are therefore key to the survival of some species (Nelson et al. 2015). However, basic questions still exist: Is complete eradication of introduced mammalian predators in mainland sanctuaries required for the recovery of lizard populations (both existing and reintroduced)? If not, what threshold level of predator control is required for healthy/stable lizard populations? How does this vary with different species of mammalian predators? Which species of mammal present the greatest risks for lizards? In this chapter, we discuss these issues for lizard conservation on the mainland using two new case studies that span more than a decade. A case study approach is used because comparable data across mainland sanctuaries are not available. Population studies of two 'at risk-declining' species (New Zealand Threat Classification, Hitchmough et al. 2016a) were compared: ornate skinks (*O. ornatum*) in ZEALANDIA, a fenced sanctuary where the skink population is recovering, and speckled skinks (*O. infrapunctatum*) adjacent to the Rotoiti Nature Recovery Project, an unfenced area with mammalian predator control. We demonstrate the difficulty of understanding the mechanisms driving lizard population dynamics in mainland sanctuaries and identify the issues that confound our understanding of the effects of predatory mammals and that warrant further research.

12.2 Case Study: Ornate Skinks in ZEALANDIA

ZEALANDIA is a 225 ha wildlife sanctuary in Wellington. Its population of ornate skinks (*O. ornatum*, Romijn 2013; Fig. 12.1) is protected by a perimeter fence, erected in 1999, designed to exclude introduced mammals. The only introduced mammals remaining within its borders are mice. Estimates of mouse abundance were initially at densities that would likely have been detrimental to lizards (e.g. 122.8 mice per 100 corrected trap nights in March 2004 for one transect line; Raewyn Empson, unpublished data; Newman 1994), but since October 2004, mice have been controlled annually (McKenzie 2007). This has resulted in lower mouse densities (mean annual peak of <22 per 100 trap nights in May–July 2009–2015 over three trap lines; mean of averaged abundances for three lines in Nov 2004–Nov 2015 was 6.6 mice per 100 trap nights compared to 68.8 mice per 100 trap nights before control started; Raewyn Empson, unpublished data; Fig. 12.2). However, peak densities for individual trap lines in May–July ranged from 0 to 59.3 mice per 100 trap nights, so in acknowledgement of the risk of high numbers of mice to some fauna, a small mouse exclosure (1 ha) was created in 2006 (McKenzie 2007; Butler et al. 2014).

Ornate skinks are one of 61 currently known endemic extant species of New Zealand skink (Chapple et al. 2009; Hitchmough et al. 2016a, b). Although they remain widespread, and occasionally locally abundant, across much of the North Island (Chapple and Hitchmough 2016), ornate skinks are ranked as ‘at risk—declining’ under the New Zealand Threat Classification System due to a loss of local populations on the mainland, and there is an expectation that their long-term future is dependent on islands remaining free of mammalian predators (Hitchmough et al. 2016a). They are medium-sized lizards (maximum SVL 87 mm; Romijn 2013) that have a wide activity period (but more actively forage during dawn and dusk) and eat a range of invertebrates (Porter 1987; Towns 1999). Ornate skinks are usually found in leaf litter or under logs and rocks and in forests, shrublands and heavily vegetated coastlines throughout the North Island and many of its offshore islands (excluding the Poor Knights Islands which have a related local endemic species, *O. roimata*; Patterson et al. 2013; Chapple and Hitchmough 2016). Their reproductive output is high relative to other New Zealand skinks, with females giving birth to up to five offspring per year (Cree 1994; Cree and Hare 2016). Both males and females are sexually mature in their second year.

Surveys of lizards in ZEALANDIA only began after the perimeter fence was erected, and mice had reached high densities, with ornate skinks first observed in 2001 (Raewyn Empson, unpublished data). In 2006–2015, pitfall trapping for skinks was conducted during eight summer sessions to evaluate population characteristics and identify the effect of mice on ornate skink populations (Romijn 2013). Ornate skink populations were monitored in two locations within the sanctuary, each subject to different predator regimes: (1) the main area of the sanctuary where mice were present and (2) in the mouse exclosure, where mice were excluded. Although mice occasionally reinvaded the mouse exclosure

Fig. 12.1 Ornate skink, *Oligosoma ornatum* (Photographer: Richard Romijn)

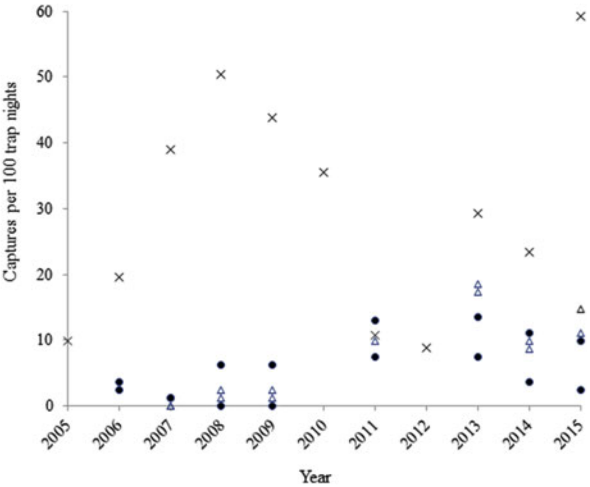


Fig. 12.2 Ornate skink (*Oligosoma ornatum*) captures in pitfall traps for each year at ZEALANDIA, Wellington. Circles represent captures in the main sanctuary, and open triangles represent captures in the mouse exclosure. Note that two replicate sites were surveyed in both the main sanctuary and in the mouse exclosure. Crosses represent the index of abundance for peak mouse numbers on a trap line adjacent to pitfall traps in the main sanctuary. Peak mouse numbers generally occurred in May, but in 2010, mouse numbers peaked in July. Skink capture rates increased significantly both in the main sanctuary and the mouse exclosure up until 2013, when skink numbers plateaued. Higher capture rates occurred in the mouse exclosure in 2013 (Romijn 2013)

(assumed to be transported by birds), they were removed by trapping when detected. All sampling sites were at similar altitudes in similar regenerating, forested vegetation dominated by native species along the west facing slopes of Te Mahanga Stream. Ornate skinks were monitored using pitfall traps, placed at 2 m intervals in a grid of nine traps, in two replicate sites within each predator regime (Hare 2012; Romijn 2013). Wire mesh was placed inside each trap to provide some protection for skinks should a mouse enter the trap. A large leaf was placed on top of the mesh to provide cover. Each trap was baited with a piece of canned pear, replaced daily through a nine-night trapping period (Romijn 2013).

Overall, 148 ornate skinks were captured (6.4 skinks per 100 trap nights). The mean capture rates of ornate skinks increased significantly (Romijn 2013) in both the main sanctuary (from 3.1 skinks per 100 trap nights in 2006 to 6.2 per 100 trap nights in 2015) and the mouse exclosure (from 0 skinks per 100 trap nights in 2006 to 13.0 per 100 trap nights in 2015). However, the highest capture rates were in 2013 in both areas (10.5 per 100 trap nights in the main sanctuary and 17.9 per 100 trap nights in the mouse exclosure). After 2013, numbers of ornate skinks levelled off in both locations, although captures in the mouse exclosure were higher than in the main sanctuary (Fig. 12.2). Mouse trapping rates were higher in the main sanctuary in 2014/2015, but this does not account for the unexpected apparent levelling off of skink numbers in the mouse exclosure (Raewyn Empson, unpublished data). The growth of the skink population was presumably achieved by maintaining an annual mouse control programme, with skink abundances peaking when mice were contained to very low levels (~10 mice per 100 trap nights) in consecutive years (Fig. 12.2). Data collected in 2013 indicated that males were larger (SVL) in the mouse exclosure compared to those in the main sanctuary, but sex ratios were not significantly different between the two sites (Romijn 2013).

The increase in captures of ornate skinks at ZEALANDIA until 2013 most likely represents, at least in part, a growing skink population that had either been totally, or partially, released from predation by introduced mammalian predators. The population growth rate was slower, and males were smaller, where skinks coexisted with mice; both factors could have long-term consequences for the population (Romijn 2013). These data are consistent with patterns of, and limits to, recovery of skinks elsewhere (e.g. Towns 1991, 1994; Newman 1994; Towns and Ferreira 2001). A plateau in captures since 2013 at both sites suggests that the population is now limited by other factors, though it seems unlikely that numbers have reached carrying capacity based on capture rates (e.g. Towns 1994; Romijn 2013).

It is possible that the recovery of skinks in ZEALANDIA has been slowed by the predation pressure of tuatara (*Sphenodon punctatus*) and birds. Tuatara were reintroduced to ZEALANDIA in 2005, with 60 placed in the mouse exclosure (McKenzie 2007). However, tuatara are not thought to be significant predators of skinks as both species co-occur on numerous islands in high densities (e.g. Phillpot 2000), and skinks are a rare occurrence in diet studies of tuatara (Walls 1981). Five volant bird species that are known to eat lizards are present in the sanctuary: kingfisher (*Todiramphus sanctus*), morepork (*Ninox novaeseelandiae*), New Zealand falcon (*Falco novaeseelandiae*), blackbird (*Turdus merula*) and the common starling (*Sturnus vulgaris*) (Van Winkel and Ji 2012). Of these, the kingfisher is likely to be a major predator as lizards have been one of the most frequent prey items brought to the nest (Hayes 1991). However, whether increasing predation by kingfishers has slowed population growth of skinks in ZEALANDIA is not known. North Island robins (*Petroica longipes*) and the North Island saddleback (*Philesturnus rufusater*) may also prey on skinks. These birds hunt for invertebrates in leaf litter and have been introduced to ZEALANDIA in the context of ecological restoration. Finally, two species of flightless bird had access to the main sanctuary but neither are not thought to have impacted skink numbers; although North Island weka (*Gallirallus australis grayi*) are known to have detrimental effects on lizard populations (Towns et al. 2002), only nine birds, which had apparently disappeared by 2010, were released into the northern part of the sanctuary (Raewyn Empson, unpublished data), so it seems unlikely that they would have had a significant effect. Little spotted kiwi (*Apteryx owenii*) would probably eat lizards they could catch, but these are unlikely to have population-level effects (reviewed in Romijn 2013).

Studies have shown that where management actions have led to an increase in bird density, there can be detrimental effects on other indigenous fauna. Watts et al. (2011) attributed declines in beetle species richness and abundance at ZEALANDIA to an increase in both mice and native birds. Sinclair et al. (2005) suggested that the decrease in invertebrate diversity on Kapiti Island after the eradication of rats was in part due to increased native bird predation. New introductions, and increased population sizes of birds and tuatara in the sanctuary, may now be the factors limiting population growth of skinks. However, further monitoring will be needed to determine the population dynamics between lizard populations and their native predators, as the population of ornate skinks now observed may be indicative of an equilibrium (or oscillation) between predator and prey.

12.3 Case Study: Speckled Skinks in the Rotoiti Nature Recovery Project

The Rotoiti Nature Recovery Project (RNRP), within New Zealand's Nelson Lakes National Park in the South Island, is a Department of Conservation 'mainland island', established to facilitate the recovery of birds. Mammalian predators (mustelids, cats, possums and rats) are controlled within, and on the periphery of, the national park using trapping and poisoning, but there is no barrier fence protecting the approximately 5000 ha area from reinvasion (Saunders 2000; Department of Conservation 2015). Predator numbers, including those not specifically targeted, decline during control pulses, but the effectiveness of control varies by year, and therefore targets for tracking rates (e.g. less than 5 % tracking rates for rats) are not always met (Long et al. 2014; Dumont 2015).

Speckled skinks (*O. infrapunctatum*; Fig. 12.3) on the periphery of the RNRP have experienced predator control since 2001 (Dumont 2015). The species is also found in the Nelson-Marlborough region and Westland (there are also seven

Fig. 12.3 Speckled skink, *Oligosoma infrapunctatum* (Photographer: Terra Dumont)

putative undescribed taxa within the *O. infrapunctatum* species complex; Hitchmough et al. 2016b; Chapple and Hitchmough 2016). Like the ornate skink, speckled skinks are listed on the New Zealand Threat Classification list as 'at risk—declining', because they have been reduced to sparsely distributed, declining populations (Dumont 2015; Hitchmough et al. 2016a). Speckled skinks are medium to large (maximum SVL of 75–106 mm depending on location) endemic lizards that inhabit densely vegetated grassland, shrubland or fern-land below 900 m (Whitaker 2000). Speckled skinks are active during the day and presumably consume a diet of invertebrates and fruit, akin to other skinks (Hare et al. 2016). Little is known about the reproductive rate of speckled skinks, but if other comparable species are used as a guide, then five offspring per female per year may be possible (Cree 1994; Dumont 2015).

Speckled skink populations were monitored between 2002 and 2011 in an area of predator control at the periphery of the RNRP zone and at an adjacent farm (not subject to predator control) to determine whether introduced mammalian predator control as part of the RNRP supported recovery of skink populations (Dumont 2015). A total of 38 pitfall traps were established in locations favourable to skinks within the RNRP zone, divided equally among two sites. Trapping effort varied throughout the study but was always conducted to maximise capture rates. A smaller amount of effort was placed on trapping skinks at the adjacent farm with no predator control, but skinks were reported as abundant in the 1960–1970s. Monitoring at the farm included an array of 50 traps divided across two sites in a grid pattern (Dumont 2015).

A total of 76 speckled skinks were captured throughout the study, with the majority being adults (96 %) captured within the RNRP sites (Fig. 12.4). Skink captures declined through time at both sites to the point where they were only barely detectable by 2012. Throughout the same period, hedgehogs (*Erinaceus europaeus*), predators not specifically targeted by the predator control programme, were the only introduced mammal species to decrease in abundance. Speckled

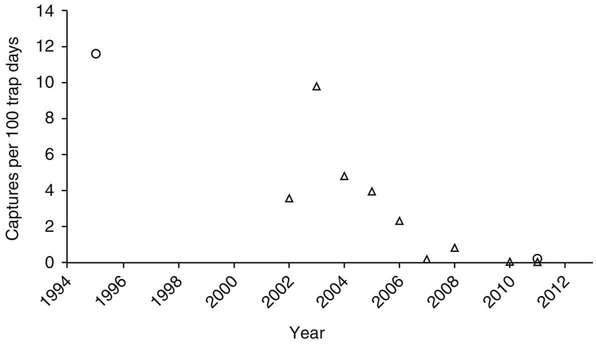


Fig. 12.4 Speckled skink (*Oligosoma infrapunctatum*) captures at Rotoiti Nature Recovery Project zone, where mammalian predators are controlled, in 2002–2011 (*triangles*), and on an adjacent farm, with no mammalian control, in 2010–2011 (*circles*) (Dumont 2015). The open circle in 1995 indicates the capture rate at the farm site prior to this study. Skink captures declined significantly through time at both sites

skink capture rates have been higher during periods of increased cat control (Dumont 2015), but the significance of cat trapping data is unclear; higher catch rates may mean fewer cats, but might also mean more cats because catch rates may simply be an index of the number of cats dispersing into the area.

This long-term study demonstrates that the current level of mammalian predator control is insufficient to protect or facilitate recovery of the speckled skink population adjacent to the RNRP zone. Dumont (2015) also collected data on two other skink species: spotted skinks, *O. lineoocellatum*, and northern grass skinks, *O. polychroma*. The life history characteristics and distribution of the latter, in particular, predict that it should be less vulnerable to predation or have a greater capacity to rebound, but the pattern of decline was common to all three species at both sites (Dumont 2015). Data for lizard populations in the RNRP zone are consistent with other studies in showing a lack of effectiveness of low- to medium-intensity predator control (Hoare et al. 2007a; Wilson et al. 2007; Reardon et al. 2012). However, introduced wasps place an additional pressure on lizards in the RNRP zone. These are present in high numbers and are likely to present a predation and competition threat for lizards (Rod Hitchmough, unpublished data).

12.4 Discussion

12.4.1 Conservation of Skinks in Mainland Sanctuaries

The study of ornate skinks within a fenced sanctuary at ZEALANDIA indicated that populations of this species may be able to increase in density only if mice are successfully controlled to low levels over consecutive years (e.g. average annual abundance approximately ≤10 mice per 100 trap nights). In contrast, research as part of the RNRP demonstrated that mammalian predator control targeted at bird recovery was insufficient to reverse declines in speckled skink populations on the periphery of the trapped area.

While populations of skinks may be able to persist and even increase in the presence of mammalian predators, as was the case when mouse density was low at ZEALANDIA, there are likely to be negative consequences for population structure. For example, mice may selectively eat larger individuals or have greater opportunity to capture these because larger individuals are limited in their ability to access smaller crevices, reducing escape prospects. Indeed, male ornate skinks in the ZEALANDIA mouse exclosure in our study were larger than those outside the exclosure. Changes in the average size of mature individuals may have a negative effect on fitness (Newman 1994). In addition, there may be unmeasured sublethal effects, such as a reduced ability to forage or thermoregulate if mice force lizards to change their behaviour to reduce predation (e.g. Herczeg et al. 2008; Hare et al. 2016; Hare and Cree 2016). Combined with direct predation effects, these factors could contribute to reduced recruitment.

Mice populations that occur in a sanctuary are protected from competition with other introduced mammals, and as a result, their populations can experience episodic outbreaks (Goldwater et al. 2012). Thus, there is a greater risk of successive population bottlenecks and other small population consequences for skink populations. These effects are likely to be similar to those experienced by birds in beech forests during masting events (Brown et al. 2015). Small populations are especially vulnerable to demographic and genetic stochasticity, environmental variability and catastrophic events (e.g. Miller et al. 2009; Towns et al. 2016, but see also O’Donnell et al. 2016). In contrast, larger populations are more robust to variation in reproductive output among cohorts, sex ratio imbalance and inbreeding. The minimum size of a population to avoid bottleneck effects in New Zealand lizards is not known, but it is possible that inbreeding depression, as a consequence of passing through a bottleneck, may be one factor preventing population recovery, even in the absence of predators. This is an area in need of further study.

The ornate skink case study also hints at the possibility that increases in non-mammalian predators restrict expansion of skink populations, because skink numbers apparently levelled off after 2013, even without mice. This suggests that other factors at this protected site were in play. In mainland sanctuaries with effective mammalian predator control, native predators increase in abundance. This is celebrated as a success for the sanctuary and rightly so. However, little is known about the ability of native predators to inhibit the recovery of remnant lizard populations. In addition, sanctuaries without introduced mammals also support large numbers of non-native birds, which either nest or roost in these safe sites. Some species are known to prey on lizards (Thompson 2000; Van Winkel and Ji 2012; Hare et al. 2016). Numerically, non-native birds that target small food items could have an enormous, yet largely unquantified, impact on lizard populations through direct predation and competition for food. Evidence from islands (e.g. Korapuki Island, Towns et al. 2016b) demonstrates that lizard populations can recover in the presence of native and non-native bird predators, but evidence on the mainland is limited. New Zealand geckos and skinks evolved for millions of years in the presence of a diverse range of predatory terrestrial and volant bird species, including both diurnal (e.g. kingfishers) and nocturnal species (e.g. owls). In contrast, introduced mammalian predators, against which native lizards appear to lack defences, pose a novel threat; these predators are more likely to hunt using olfactory cues rather than the visual and auditory cues used by avian predators. Finally, larger populations of lizards are unlikely to experience the same negative impacts of bird predation.

Predator control at an unfenced site on the periphery of the RNRP zone was insufficient for protection of lizards. Our research on speckled skinks supported the generally well-held view that terrestrial, large-bodied lizards are extremely vulnerable to mammalian predation (e.g. Whitaker's skink; Hoare et al. 2007a). To date, predator control in unfenced sites on the mainland has only been successful for lizard recovery when it has been specifically targeted for lizard recovery, and even so, skinks only recovered in core areas of predator control and not in the peripheral areas (e.g. grand, *O. grande*, and Otago, *O. otagense*, skinks; Reardon et al. 2012). Intensive small-scale control of predatory mammals, targeted for lizard recovery, is needed to prevent further species loss, particularly where species survival and medium-term persistence is possible with small, isolated populations. Such minimum scale and minimum cost management is vital in order to gain some level of security from extinction in the short term. However, better techniques that are applicable for the sustainable management of lizards at larger habitat/landscape scales, and which are robust to outbreak or reinvasion problems, are required.

Smaller and more common species of skinks within the RNRP were also found to be in decline (Dumont 2015). Nonetheless, control measures such as fencing and trapping can increase capture rates for some common species (e.g. McCann's skink *O. maccanni*, southern grass skink *O. polychroma*; Wilson et al. 2007, 2017). This is probably because the more common species often have life history characteristics, such as higher reproductive productivity (Cree 1994; Cree and Hare 2016) that can enable populations to bounce back after episodic predator increases have been contained (O'Donnell and Hoare 2012). However, the ability of some skink species to respond to predator control does not mean that they are immune from local extinction. Population recovery may be constrained by small population size and distribution at the time of the bottleneck, relatively low reproductive output (Cree 1994; Cree and Hare 2016) and other habitat (e.g. variation in population size with habitat, overlapping retreat sites with mammals or burning and cultivation regimes) or time variables (e.g. seasonal and long-term climatic variation) that could have additive or synergistic effects on limits to recovery. Analogies of how the recovery of a skink population may be limited on the mainland, even with predator control, can be drawn from density estimates from islands that have never had mammalian predators or competitors and where skink populations are presumably at carrying capacity and can reach extremely high numbers (e.g. estimated population density of 3700/ha for spotted skinks, *O. lineoocellatum* on North Brother Island; Phillpot 2000). Reliable information on long-term responses of populations of more common (and smaller-bodied) species in areas of mammalian predator control is needed. This will enable managers to identify threshold population sizes (or tracking indices) of mammal species that allow net population growth of lizards. Such information is crucial for decision-making on levels of mammalian predator control if it is not possible to eradicate predatory mammals from an ecosystem.

12.4.2 Conservation of Geckos in Sanctuaries

The implications of predator control for geckos are less clear than they are for skinks. We assume that gecko responses will be similar to those of skinks, but their recovery is likely to be slower because geckos have a lower reproductive output (maximum of two offspring per adult female per annum for small, warm-climate species, decreasing to one or two every second year for larger or cooler-climate species), and longer time to maturity (ranging from 2 to 8 years depending on temperature and body size) (Cree 1994; Cree and Hare 2016).

Data on gecko population dynamics in New Zealand are limited and, for the mainland, predominantly based on sightings per unit search effort, although recent work into use of artificial cover objects has improved detection (Bell 2009). Small capture numbers and too few recaptures to adequately estimate population size present difficulties for managing these populations (e.g. Hoare et al. 2013). Trends over time are largely based on capture data from islands after mammal eradications since there were no, or few, gecko sightings prior to eradication but then more reliable sightings post-eradication. The behaviour of some species has allowed them to survive without detection since they spend more time in trees or on cliffs, thereby also avoiding largely ground-based mammalian predators (Hoare et al. 2007b). Additional detection difficulties arise as a result of the cryptic colouration and behaviour of geckos and their use of largely inaccessible arboreal habitats. Low reproductive rates (Cree 1994) can also delay detection in the period immediately after eradication of mammals as populations take time to recover. For example, despite pre-eradication surveys, it took 17 years after mammalian predators were eradicated from Kapiti Island, off the North Island coast, before gold-striped geckos (*Woodworthia chrysosiretica*) were first observed (Richard Romijn, unpublished data). Similarly, 12 years after eradication of all pest mammals from Codfish Island/Whenua Hou, 300 h of targeted spotlighting detected only three jewelled geckos (*Naultinus gemmeus*). Cloudy geckos (*Mokopirirakau nebulosus*) were not encountered during the targeted search, though they have been observed occasionally since the searches, confirming their persistence on the island (James Reardon, unpublished data).

Mainland examples of gecko population trends are scarce but important to note. For example, a Duvaucel's gecko (*Hoplodactylus duvaucelii*) was discovered on Maungatautari, a fenced mountain sanctuary in the Waikato region, North Island, 4 years after introduced mammals were eradicated (Morgan-Richards et al. 2016). It is possible that this observation resulted from behavioural changes by this species, rather than a population-level response to eradication of mammals due to the K-selected life history characteristics of Duvaucel's gecko (Cree 1994; Hoare et al. 2007b). The effects of mammalian predator control on skinks likely also apply to geckos. In other words, total, or at least very strict, control of mammalian predators to low levels over sustained periods is probably required for gecko recovery.

12.4.3 Research Directions and Management Challenges

To limit or mitigate the effects of introduced mammalian predators on lizards, basic biological information, and how this might vary across the distribution of each species, is needed. However, this is lacking for most species. Distributional information is limited for all New Zealand lizard species, and extant population information often hints at a larger former distribution (e.g. Whitakers skink, Worthy 1987; Hoare et al. 2007a; Worthy 2016). For example, where lizards have apparent specific ecotypes, such as those of alpine specialists, it is unclear whether they are relicts or simply represent edge habitat of their former (pre-mammal) ranges (DOC 2016), a pattern that has been found in other groups of animals (Beauchamp and Worthy 1988). The distributions of the Cascade gecko (*Mokopirirakau* 'Cascades') and the Takitimu gecko (*M. cryptozoicus*), both once assumed to be alpine specialists, also include sightings in locations well below subalpine altitudes. This provides considerable evidence for previously broader altitudinal distributions. Ecological research into climate-induced physiological limitations that will enhance knowledge of potential distributions and guide management for detection and restoration is needed (Chapple and Hitchmough 2016; Hare and Cree 2016). In addition, more robust data on life history characteristics, and intrinsic rates of increase, would help inform the time needed to detect species before attempts are made to reintroduce missing species (Cree and Hare 2016). In most instances, data are likely to be both species and situation dependent, requiring more research effort into the biology of New Zealand lizards than has been the case to date.

The potential rise in predation on lizards by increased populations of predatory birds (both native and non-native) as a result of successful control of mammalian predators is not the only barrier to lizard recovery, particularly in mainland sanctuaries. An additional challenge to the recovery of lizards, albeit at this point only speculative, is the potential impact from increased abundance and distribution of introduced social insects including wasps and Argentine ants (*Linepithema humile*), either from direct effects on survival or indirect effects on food sources. Invertebrates are strongly negatively affected by wasps (Lester et al. 2013), and losses of lizards in captivity have been attributed to wasps and ants (Rod Hitchmough, unpublished data). Since both lizards and introduced wasps also consume nectar and invertebrates, it seems reasonable to expect there are downstream effects on lizards in areas with large wasp populations (Towns 2002). Wasps have increased in abundance and diversity in the last 90 years (Lester et al. 2013) and are particularly problematic in honeydew beech forest systems (e.g. Beggs 2001). The RNRP zone, where our case study on speckled skinks was based, has a serious problem with high wasp densities, dating from the invasion of common wasps (*Vespula vulgaris*) in the 1980s. Wasp poisoning is underway in the RNRP zone and other sites around New Zealand (Harper et al. 2016). Identifying the detrimental effects of wasps on lizard populations will be problematic due to concurrent mammalian predator control, and the nature of trying to assess effects in complex natural systems under adaptive management. A significant advancement in recent times has been the apparently successful control of wasps using toxic bait stations, which potentially offers an effective and sustainable management tool (Harper et al. 2016). This presents an opportunity to conduct controlled experiments to test the impacts of wasps and ants on lizards. These would be best done in areas adjacent to current mainland island conservation projects so that the level of any observed effects can be separated from those caused by mammalian predators.

Research to date suggests that predation by mammalian predators is by far the most important factor limiting lizard populations (e.g. Lettink et al. 2010), highlighting the importance of mammalian predator control. Nonetheless, other management actions also offset the causes of decline in lizard populations. These include wasp and ant control and habitat manipulation to increase structural complexity, thereby improving survival by providing protection from extreme environments and predators (Sinclair et al. 1998; Norbury et al. 2015). However, because mice are likely to remain in most mainland sanctuaries, increasing habitat and refuges for terrestrial lizards also benefits small rodents, thereby potentially increasing predation risk. All activities regarded as habitat enhancements should be confirmed via an experimental approach rather assuming that they are, in fact, improvements. Finally, developing effective methods of lizard conservation in mainland sanctuaries would not only aid the recovery of the full range of native species in such areas but could also contribute to the development of novel, or more refined, solutions to maintaining stable populations of lizards. This could be particularly valuable in other areas of the mainland where predator control is currently not feasible or performed at an inadequate scale. Biodiversity in mainland sanctuaries could be enormously improved if lizard conservation was afforded the same attention as that of birds.

Acknowledgements Thanks to the friends of Rotoiti volunteers, Diana McMahon, Eric Dumont, Sirin Gnadeberg and Richard Meutstege; Ingrid McConchie for site access and Genevieve Taylor, Kimberly Parlane, Tamsin Bruce, Sally Leggett, Petrina Carter, Grant Harper, Elena Moltchanova, Laura Azzani, Matt Hanson, the Department of Conservation and friends of Rotoiti for project support. Our work was conducted under the following permits: Department of Conservation (NM–29621–FAU, WE/31544-FAU, WE112/RES, WE/297/RES, WE/340/RES, WE/33952/CAP), University of Canterbury Animal Ethics (2010/28R) and Victoria University of Wellington (2003R16-06, 2005R11-08, 2008R14, 2012R11). The Todd Foundation Award for Excellence, Federation of Graduate Women Trust Award, University of Canterbury Alumni Association Scholarship, the BAYER Boost Scholarship and the University of Canterbury part funded this research. We thank David Towns for reviewing an earlier version of this chapter.

References

Beauchamp AJ, Worthy TH (1988) Decline in the distribution of takahe (*Porphyrio mantelli*): a re-examination. J R Soc N Z 18(1):103–118

Beggs JR (2001) The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. Biol Conserv 99:17–28

Bell TP (2009) A novel technique for monitoring highly cryptic lizard species in forests. Herpetol Conserv Biol 4(3):415–425

Brown K, Elliot G, Innes J, Kemp J (2015) Ship rat, stoat, and possum control on mainland New Zealand: an overview of techniques, successes and challenges. Department of Conservation, Wellington, 36p

Burns B, Innes J, Day T (2012) The use and potential of pest-proof fencing for ecosystem restoration and fauna conservation in New Zealand. In: Somers MJ, Hayward MS (eds) Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? Springer, New York, pp 65–90

Butler D, Lindsay T, Hunt J (2014) Paradise saved: the remarkable story of New Zealand's wildlife sanctuaries and how they are stemming the tide of extinction. Random House, Auckland, 320p

Caut S, Casanovas JG, Virgos E, Lozano J, Witmer GW, Courchamp F (2007) Rats dying for mice: modelling the competitor release effect. Austral Ecol 32:858–868

Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Daugherty CH, Ritchie PA (2009) Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). Mol Phylogenet Evol 52:470–487

Cree A (1994) Low annual reproductive output in female reptiles from New Zealand. N Z J Zool 21:351–372

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Crooks KR, Soulé ME (1999) Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566

Department of Conservation (2015) http://www.doc.govt.nz/our-work/mainland-islands/rotoiti/. Accessed 11 Nov 2015

Department of Conservation (2016) http://www.doc.govt.nz/our-work/reptiles-and-frogs-distribution/atlas/. Accessed 21 Jan 2016

Dumont CT (2015) An investigation into declining skink populations and their behavioural responses to introduced mammalian predators. Masters of Science thesis, University of Canterbury, Christchurch, 154p

Goldwater N, Perry GLW, Clout MN (2012) Responses of house mice to the removal of mammalian predators and competitors. Austral Ecol 37:971–979

Hare KM (2012) Herpetofauna: pitfall trapping version 1.0. Inventory and monitoring toolbox: herpetofauna DOCDM-760240, Department of Conservation, Wellington, 22p

Hare KM, Cree A (2016) Thermal and metabolic physiology of New Zealand lizards. Chap. 9. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hare KM, Chapple DG, Towns DR, van Winkel D (2016) The ecology of New Zealand's lizards. Chap. 6. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Harper GA, Joice N, Kelly D, Toft R, Clapperton BK (2016) Effective distances of wasp (*Vespula vulgaris*) poisoning using clustered bait stations in beech forest. N Z J Ecol 40:65–71

Hayes LM (1991) Behaviour of New Zealand kingfishers feeding chicks. Notornis 38:73–79

Herczeg G, Herrero A, Saarikivi J, Gonda A, Jantti M, Merila J (2008) Experimental support for the cost–benefit model of lizard thermoregulation: the effects of predation risk and food supply. Oecologia 155(1):1–10

Hitchmough R, Barr B, Monks J, Lettink M, Reardon J, Tocher M, van Winkel D, Rolfe J (2016a) Conservation status of New Zealand reptiles, 2015, New Zealand threat classification series. Department of Conservation, Wellington

Hitchmough RA, Patterson GB, Chapple DG (2016b) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hoare JM, Adams LK, Bull LS, Towns DR (2007a) Attempting to manage complex predator-prey interactions fails to avert imminent extinction of a threatened New Zealand skink population. J Wildl Manage 71:1576–1584

Hoare JM, Pledger S, Nelson NJ, Daugherty CH (2007b) Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. Biol Conserv 136:510–519

Hoare JM, Melgren P, Chavel EE (2013) Habitat use by southern forest geckos, *Mokopirirakau* “Southern Forest” in the Catlins, Southland. N Z J Zool 40(2):129–136

Innes J, Saunders A (2011) Eradicating multiple pests: an overview. In: Veitch CR, Clout MN, Towns DR (eds) Island invasives: eradication and management. IUCN, Gland, pp 177–181

Innes J, Kelly D, McC Overton J, Gillies C (2010) Predation and other factors currently limiting New Zealand forest birds. N Z J Ecol 34(1):86–114

Jones C, Norbury G, Bell T (2013) Impacts of introduced European hedgehogs on endemic skinks and weta in tussock grassland. Wildl Res 40:36–44

Lester PJ, Beggs JR, Brown RL, Edwards ED, Groenteman R, Toft RJ, Twidle AM, Ward DF (2013) The outlook for control of New Zealand’s most abundant, widespread and damaging invertebrate pests: social wasps. N Z Sci Rev 70(4):56–62

Lettink M, Norbury G, Cree A, Seddon PJ, Duncan RP, Schwarz CJ (2010) Removal of introduced predators, but not artificial refuge supplementation, increases skink survival in coastal duneland. Biol Conserv 143:72–77

Long J, Waite J, Joice N, Grose T (2014) Rotoiti nature recovery project annual report 2013–14, Nelson lakes mainland island, Nelson Lakes National Park, 85p

McKenzie KL (2007) Returning tuatara (*Sphenodon punctatus*) to the New Zealand mainland. Master of Science thesis, Victoria University of Wellington, Wellington, 82p

Miller KA, Chapple DG, Towns DR, Ritchie PA, Nelson NJ (2009) Assessing genetic diversity for conservation management: a case study of a threatened reptile. Anim Conserv 12:163–171

Morgan-Richards M, Rheyda Hinlo M, Smuts-Kennedy C, Innes J, Ji W, Barry M, Brunton D, Hitchmough RA (2016) Identification of a rare gecko from North Island New Zealand, and genetic assessment of its probable origin: a novel mainland conservation priority? J Herpetol 50:77–86

Nelson NJ, Hitchmough R, Monks JM (2015) New Zealand reptiles and their conservation. In: Stow A, Maclean N, Holwell GI (eds) Austral Ark: the state of wildlife in Australia and New Zealand. Cambridge University Press, Cambridge, pp 382–404

Newman DG (1994) Effect of a mouse *Mus musculus* eradication programme and habitat change on lizard populations on Mana Island, New Zealand, with special reference to McGregor’s skink, *Cyclodina macgregori*. N Z J Zool 21:443–456

Norbury G, Byrom A, Pech R, Smith J, Clarke D, Anderson D, Forrester G (2013) Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. Ecol Appl 23:1707–1721

Norbury G, van den Munckhof M, Neitzel S, Hutcheon A, Reardon J, Ludwig K (2014) Impacts of invasive house mice on post-release survival of translocated lizards. N Z J Ecol 38:322–327

Norbury GL, Pech RP, Byrom AE, Innes J (2015) Density-impact functions for terrestrial vertebrate pests and indigenous biota: guidelines for conservation managers. Biol Conserv 191:409–420

O’Donnell CFJ, Hoare JM (2012) Monitoring trends in skink sightings from artificial retreats: influences of retreat design, placement period, and predator abundance. Herpetol Conserv Biol 7(1):58–66

O’Donnell CFJ, Richter S, Dool S, Monks JM, Kerth G (2016) Genetic diversity is maintained in the endangered New Zealand long-tailed bat (*Chalinolobus tuberculatus*) despite a closed social structure and regular population crashes. Conserv Genet 17(1):91–102

Patterson GB, Hitchmough RA, Chapple DG (2013) Taxonomic revision of the ornate skink (*Oligosoma ornatum*; Reptilia: Scincidae) species complex from northern New Zealand. Zootaxa 3736(1):54–68

Phillpot P (2000) The skinks of North Brother Island: abundance, habitat use and species interactions. Master of Science thesis, Victoria University of Wellington, 138p

Porter R (1987) An ecological comparison of two *Cyclodina* skinks (Reptilia: Lacertilia) in Auckland, New Zealand. N Z J Zool 14:493–507

Reardon JT, Whitmore N, Holmes KM, Judd LM, Hutcheon AD, Norbury G, Mackenzie DI (2012) Predator control allows critically endangered lizards to recover on mainland New Zealand. N Z J Ecol 36:141

Romijn RL (2013) Can skinks recover in the presence of mice? Bachelor of Science (Honours) thesis, Victoria University of Wellington, Wellington, 51p

Saunders A (2000) A review of Department of Conservation mainland restoration projects and recommendations for further action. Department of Conservation, Wellington, 219p

Sinclair ARE, Pech RP, Dickman CR, Hik D, Mahon P, Newsome AE (1998) Predicting effects of predation on conservation of endangered prey. Conserv Biol 12(3):564–575

Sinclair L, McCartney J, Godfrey J, Pledger S, Wakelin M, Sherley G (2005) How did invertebrates respond to eradication of rats from Kapiti Island, New Zealand? N Z J Ecol 32:293–315

Thompson MB (2000) *Oligosoma* spp. (New Zealand skinks) predation. Herpetol Rev 31:175

Tingley R, Hitchmough RA, Chapple DG (2013) Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol Conserv 165:62–68

Towns DR (1991) Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: the kiore (*Rattus exulans*). J R Soc N Z 21:119–136

Towns DR (1994) The role of ecological restoration in the conservation of Whitaker's skink (*Cyclodina whitakeri*), a rare New Zealand lizard (Lacertilia: Scincidae). N Z J Zool 21:457–471

Towns DR (1999) Cyclodina spp. skink recovery plan, 1999–2004, Threatened species recovery plan 27. Department of Conservation, Wellington, 75p

Towns DR (2002) Interactions between geckos, honeydew scale insects and host plants revealed on islands in northern New Zealand, following eradication of introduced rats and rabbits. In: Veitch CR, Clout MN (eds) Turning the tide: the eradication of invasive species. IUCN, Gland, pp 329–335

Towns DR, Broome KG (2003) From small Maria to massive Campbell: forty years of rat eradications from New Zealand Islands. N Z J Zool 30:377–398

Towns DR, Daugherty CH (1994) Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation. N Z J Zool 21(4):325–339

Towns DR, Ferreira S (2001) Conservation of New Zealand lizards (Lacertilia: Scincidae) by translocation of small populations. Biol Conserv 98(2):211–222

Towns DR, Daugherty CH, Cree A (2001) Raising the prospects of a forgotten fauna: a review of 10 years of conservation effort for New Zealand reptiles. Biol Conserv 99:3–16

Towns DR, Neilson KA, Whitaker AH (2002) North Island Oligosoma spp. skink recovery plan, 2002–2012, Threatened species recovery plan 48. Department of Conservation, Wellington, 62p

Towns DR, Hitchmough RA, Perrott J (2016a) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? Chap. 11. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Towns DR, Borrelle SB, Thoresen J, Buxton RT, Evans A (2016b) Mercury Islands and their role in understanding seabird island restoration. N Z J Ecol 40(2):235–249

Towns DR, Miller KA, Nelson NJ, Chapple DG (2016) Will translocations to islands reduce extinction risk for reptiles? Case studies from New Zealand. Biol Conserv doi:10.1016/j.biocon.2016.04.024

Van Winkel D, Ji W (2012) Evidence of lizard predation by New Zealand kingfishers (*Todiramphus sanctus vagans*) and potential implications for threatened species translocations. N Z J Zool 39(3):201–208

Walls GY (1981) Feeding ecology of the tuatara (*Sphenodon punctatus*) on Stephens Island, Cook Strait. N Z J Ecol 4:89–97

Watts CH, Armstrong DP, Innes J, Thornburrow D (2011) Dramatic increases in weta (Orthoptera) following mammal eradication on Maungatautari—evidence from pitfalls and tracking tunnels. N Z J Ecol 35:261–272

Wedding CJ (2007) Aspects of the impacts of mouse (*Mus musculus*) control on skinks in Auckland, New Zealand. Master of Science thesis, Massey University, Auckland, 133p

Whitaker T (2000) Lizards of Nelson and Marlborough: a field key. Nelson/Marlborough Conservancy, Department of Conservation, Wellington, 20p

Wilson DJ, Clarke DA, Mulvey RL, Reardon JT (2017) Assessing and comparing population densities and indices of skinks under three predator management regimes. N Z J Ecol 41(1)

Wilson DJ, Mulvey RL, Clark RD (2007) Sampling skinks and geckos in artificial cover objects in a dry mixed grassland-shrubland with mammalian predator control. N Z J Ecol 31:169–185

Worthy TH (1987) Osteological observations on the larger species of the skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. N Z J Zool 14:219–229

Worthy TH (2016) A review of the fossil record of New Zealand lizards. Chap. 3. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapter 13
Origin, Spread and Biology of the Invasive Plague Skink (*Lampropholis delicata*) in New Zealand

David G. Chapple, James T. Reardon, and Joanne E. Peace

Abstract The plague skink (*Lampropholis delicata*) is the only reptile species that has established, and subsequently become invasive, in New Zealand. Native to eastern Australia, the plague skink was first detected in south Auckland in the mid-1960s. A molecular study has identified the source population for the introduction as inland northern New South Wales, near Tenterfield. The plague skink has now spread across the majority of the North Island via human-assisted jump dispersal. It has the potential to extend its distribution to the entire North Island, apart from the Central Plateau region, and also to the Nelson-Marlborough and Canterbury regions of the South Island. Sexual dimorphism exists in plague skink populations in New Zealand, with females having larger body size and interlimb lengths and males having longer and broader heads. Population density appears to influence body size in males. Plague skinks in New Zealand lay eggs, often communally, in sheltered microhabitats, with the eggs hatching in February and March. The mean clutch size varies among populations, and clutch size is positively related to female body size. Plague skinks utilise a wide variety of habitats, both natural and modified, are diurnal and are opportunistic insectivores. The evidence for the impact of the plague skink on the native New Zealand biota is currently equivocal. The plague skink has recently spread to conservation-sensitive offshore islands in the Hauraki Gulf, including Great Barrier Island, promoting additional research into eradicating or mitigating the spread of the species within New Zealand.

Keywords Biosecurity • Delicate skink • Invasive species • New Zealand • Plague skink

---

D.G. Chapple (✉)
School of Biological Sciences, Monash University, 25 Rainforest Walk, Clayton, VIC 3800, Australia
e-mail: David.Chapple@monash.edu

J.T. Reardon
Department of Conservation, Herpetology and Pest Threats, Te Anau 9640, New Zealand

J.E. Peace
School of Biological Sciences, University of Auckland, Auckland 1142, New Zealand

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_13

13.1 Introduction

Invasive lizards have the potential to impose a broad range of ecological and evolutionary impacts in their introduced range (Lever 2003; Kraus 2009, 2015). Exotic lizard species are primarily moved around the globe via human-mediated transportation via the pet trade (deliberate introductions, escape/release from captivity) or as stowaways in freight and cargo (Kraus 2009; Chapple et al. 2016). Increasing globalization over the last few decades, and the associated expansion of international trade, has resulted in a sharp rise in the number of exotic lizard species being introduced to non-native regions (Kraus 2009). Lizards possess several traits that enhance their ability to remain undetected in freight and cargo, including small body size, cryptic nature, desiccation-resistant eggs, the ability to withstand temperature fluctuations and low metabolic rate that allows them to survive long periods without food and water (Kraus 2009; Toy and Newfield 2010). Invasive lizards therefore represent a significant threat to New Zealand's diverse, endemic lizard fauna (~104 extant species: ~61 skink and ~43 gecko species; Tingley et al. 2013; Hitchmough et al. 2016a, b; Chapple and Hitchmough 2016; Towns et al. 2016).

Although 99 lizard species (across 13 different families) have been intercepted by biosecurity agencies entering New Zealand (Chapple et al. 2016), the plague skink (*Lampropholis delicata*) is the only lizard species that has successfully established and subsequently become invasive in the country (Lever 2003; Kraus 2009; Chapple et al. 2013a, b). The plague skink (known as the delicate skink in its native range and also as the rainbow skink in New Zealand parts of its invasive range) is a small-sized species (adult snout-vent length [SVL] 35–55 mm) that is native to eastern Australia. It occurs across 26° of latitude in its native Australian range from northern Queensland to Tasmania and extends as far west as south-eastern South Australia (Chapple et al. 2011a; Wilson and Swan 2013; Cogger 2014; Fig. 13.1). The plague skink occurs across a range of moist habitats in Australia but thrives in disturbed habitats and suburban gardens (Wilson and Swan 2013; Moule et al. 2016). It reaches sexual maturity in 1 year and has a life span of approximately 2–4 years (Greer 1989). It is oviparous and often produces large communal egg nests that are positioned under rocks, logs and vegetation (Greer 1989; Cheetham et al. 2011; Doody and Paull 2013). The plague skink is the only species of Australian lizard that is invasive overseas (Lever 2003; Kraus 2009) and, in addition to New Zealand, has established populations in the Hawaiian Islands (Baker 1979) and on Lord Howe Island (Hutchinson et al. 2005; Schulz 2009; Chapple et al. 2014; Moule et al. 2015).

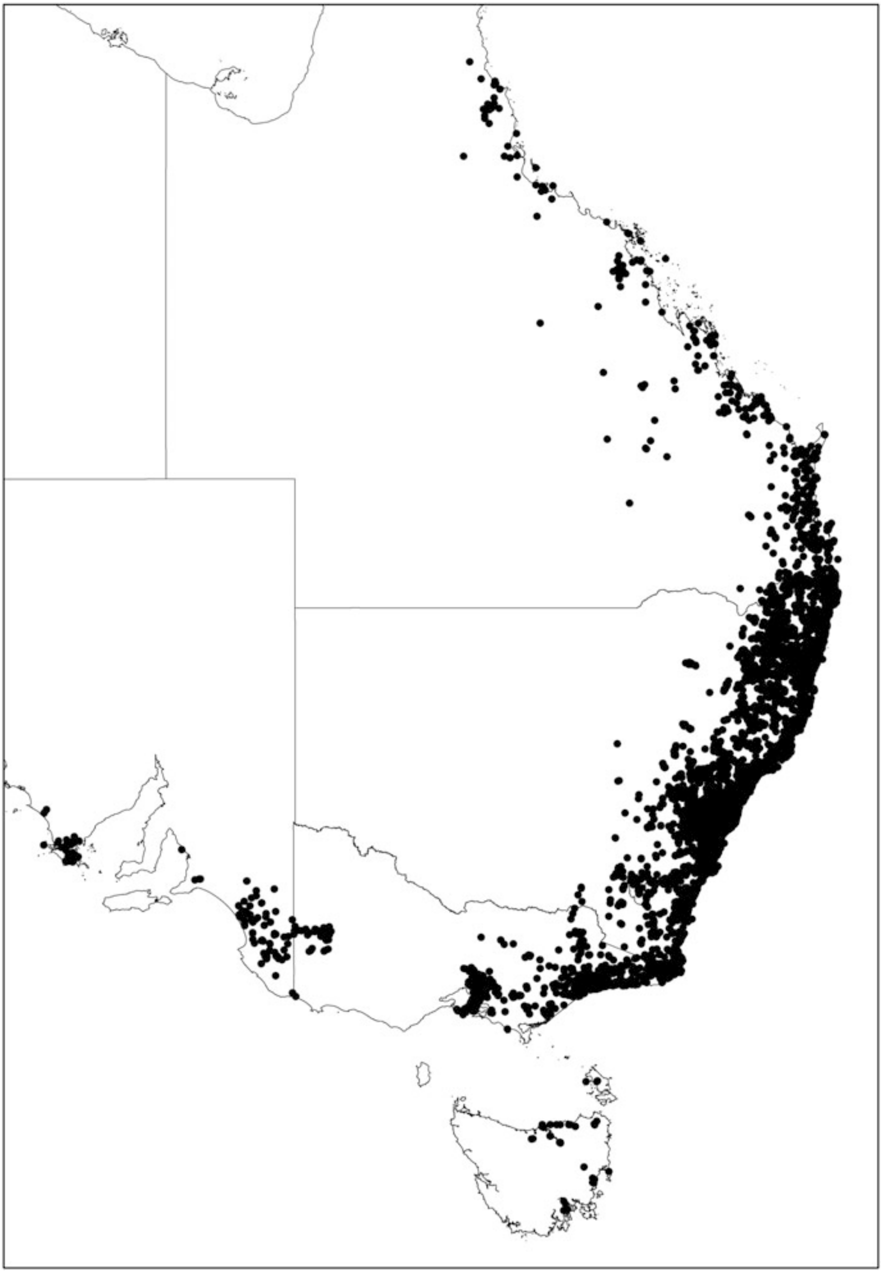


Fig. 13.1 Native Australian range of the plague skink (*Lampropholis delicata*). The distribution of the plague skink follows Tingley et al. (2016) and is based on the Atlas of Living Australia (www.ala.org.au) and the records of all major Australian museums

13.2 Introduction History and Post-establishment Spread in New Zealand

The plague skink has been present in New Zealand for at least 50 years. It was first detected in the country in the mid-1960s at the Otahuhu rail yards in south Auckland (A.H. Whitaker pers. comm. in Lever 2003), and it appears to have been accidentally introduced into New Zealand, possibly in a shipment of wooden railway sleepers from Australia (as eggs or juvenile/adult individuals; A.H. Whitaker pers. comm. in Lever 2003; Chapple et al. 2013a). The number of initial founders was likely small, as most lizard stowaways are transported individually or in small groups (Chapple et al. 2013b, 2016), and the incursion was restricted to the Auckland region for ~15 years (Lever 2003). However, its subsequent spread across the North Island was rapid, first into the Waikato [Hamilton, 1978; Paeroa, 1984], Bay of Plenty [Tauranga: 1978] and Coromandel Peninsula regions [Waikawau Bay: 1984] (West, 1979; Lever 2003; Fig. 13.2). Over the past two decades, the plague skink has spread southwards to the lower North Island [Wanganui, 1996; Palmerston North, 2009] and southern Bay of Plenty [Whakatane, 2003; Edgecumbe, 2007] and northwards into Northland [Whangarei, 2002; Dargaville, 2007; Kaitaia, 2008] (Peace 2004; Chapple et al. 2013a; New Zealand Herpetofauna database 2015; Fig. 13.2).

Although the source region for the initial introduction of the plague skink into New Zealand was initially thought to be Sydney (A.H. Whitaker pers. comm. in Lever 2003), recent molecular data (mitochondrial DNA sequence data; mtDNA) indicated that the founders originated from a forestry region of inland northern New South Wales, near Tenterfield (Chapple et al. 2013a). Substantial phylogeographic structure within the native Australian range (nine distinct genetic lineages and unique haplotypes in each locality sampled; Chapple et al. 2011a) enabled the seven haplotypes present in the introduced New Zealand populations to be traced back to a single Australian source region (Chapple et al. 2013a). Whilst it is possible that the plague skink was introduced from Australia on multiple occasions from the same source region, its ability to produce large communal nests (often involving 100+ eggs; Greer 1989; Chapple et al. 2014) means that all seven haplotypes could have been introduced in a single communal nest. Research is currently being conducted to determine whether the introduction of the plague skink into New Zealand was associated with a decrease in neutral genetic variation (i.e. microsatellite markers; Chapple and Thompson 2009; Chaplin 2013; DGC unpublished data).

The plague skink is particularly adept at dispersing via human-mediated transportation, especially compared to other widespread Australian species (e.g. *L. guichenoti*, Chapple et al. 2011a, b, c, 2013b; Cromie and Chapple 2012). Indeed, it is the fifth most intercepted lizard species (behind *Hemidactylus frenatus*, *Lepidodactylus lugubris*, *Gehyra oceanica* and *Hemidactylus platyurus*) by New Zealand biosecurity agencies (Chapple et al. 2016). The plague skink exhibits high levels of intraspecific behavioural variation (Michelangeli et al. 2016; Moule

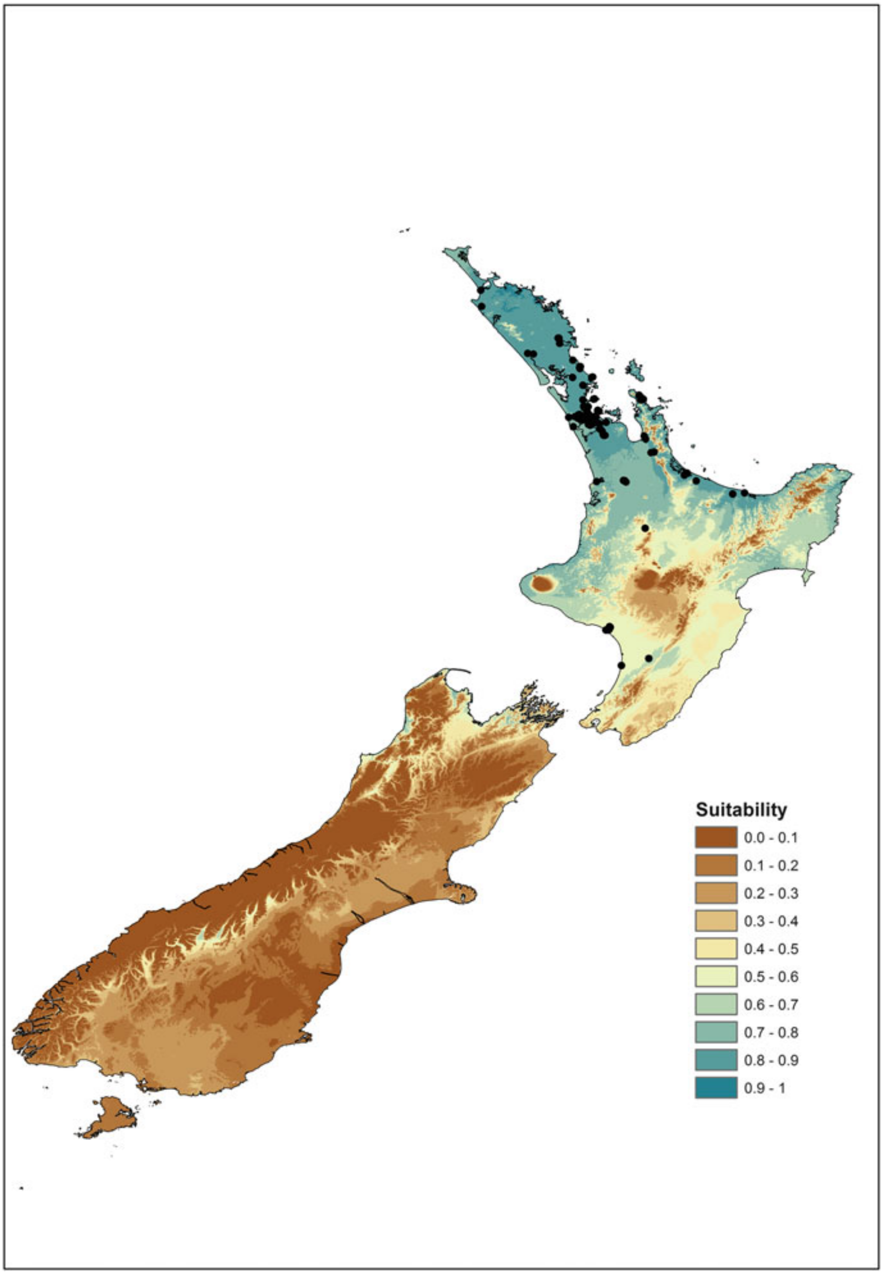


Fig. 13.2 Current distribution of the plague skink (*Lampropholis delicata*) in New Zealand (distributional data follows Tingley et al. 2016 and the New Zealand Herpetofauna database 2015). The potential distribution of the plague skink in New Zealand is indicated (adapted with permission from Tingley et al. 2016)

et al. 2016) and several behavioural traits that may increase its propensity for human-assisted dispersal (Chapple et al. 2011b, 2012; Cromie and Chapple 2012). For instance, the plague skink is highly exploratory, which may increase its likelihood of getting into freight and cargo but also has a tendency to actively hide and seek shelter, which could enhance its ability to remain undetected during transit (Chapple et al. 2011b; Cromie and Chapple 2012).

The spread of the plague skink throughout New Zealand appears to be driven primarily through human-assisted 'jump' dispersal (sensu Wilson et al. 2009), rather than natural range expansion (Chapple et al. 2013b). This has led to the 'spot fire' spread of the species across New Zealand, with human-assisted transportation of the species from the Auckland region to other locations in the country (as outlined above). Chapple et al. (2013b) conducted genetic analyses on tissue samples from the 79 plague skink specimens intercepted by the New Zealand biosecurity agency (Ministry for Primary Industries, MPI) between 2001 and 2009. Since the established New Zealand plague skink population has known mtDNA haplotypes, it was possible to assign biosecurity interceptions to either new arrivals into the country direct from Australia (and their specific point of origin) or post-border spread within New Zealand. The established New Zealand population is the major source of stowaways spreading across the country (84 % of interceptions), whereas only 16 % are new arrivals from Australia (generally originating from the region between Brisbane and Sydney; Chapple et al. 2013b; Table 13.1). Plague skinks arrive in New Zealand in freight and cargo via both air and sea transport routes (Table 13.1), but 30 % of interceptions involved the post-border spread of plague skinks (via road, rail and air transport) from the Auckland region to areas beyond the species' established New Zealand range (Chapple et al. 2013b; Table 13.2). Plague skink stowaways are typically solitary, adult individuals that are alive when detected and intercepted during the cooler months of the year (Chapple et al. 2013b; Tables 13.1 and 13.2).

Although the plague skink has been established in New Zealand for at least 50 years, it is still spreading across the country and is yet to fulfil its potential distribution (Chapple et al. 2013b; Tingley et al. 2016; Fig. 13.2). The species has not yet exhibited evidence of niche expansion following its introduction to New Zealand and has failed to colonise some environmental niches (16 %) in New Zealand that are equivalent to those occupied in its native Australian range (termed niche 'unfilling'; Tingley et al. 2016). Predictive environmental niche modelling indicates that the plague skink has the capacity to expand across the entire North Island, apart from the Central Plateau region (Tingley et al. 2016; Fig. 13.2). In addition, there is moderate potential for the plague skink to establish in parts of the South Island, most likely in the Nelson-Marlborough and Canterbury regions (Tingley et al. 2016; Fig. 13.2). Thus, conservation and biosecurity protocols should be developed to prevent, or limit, the continued spread of the plague skink throughout New Zealand (Chapple et al. 2013b, 2016; Wairepo 2015). Indeed, it would seem that over the past decade, the rate of spread of plague skinks across the islands of the Hauraki Gulf has accelerated, with the skinks now apparently established on Kawau and Rotoroa Islands. The more recent incursion

Table 13.1 Details of the plague skink (*Lampropholis delicata*) specimens intercepted entering New Zealand direct from Australia

	Interception					Lizard			Origin	
Sample Code	Location	Month	Transport method	Border or post-border	Cargo type	SVL (mm)	Adult?	Alive?	Predicted	Confirmed
LDN01	Wellington	Oct	Air	Post-border	Personal effects	28	N	Alive	Sydney	Sydney
LDN06	Auckland	March	Sea	Post-border	Shipping container (cosmetics, food)	30	N	Alive	Sydney	Sydney
LDN07	Auckland	June	Air	Border	Personal effects	39	Y	Alive	Brisbane	Gold Coast-Lamington NP
LDN23	Auckland	June	Sea	Post-border	Shipping container (light fittings)	30	N	Alive	Nth Sydney (Brookvale)	Nth NSW coast-Wyong
LDN26	Wellington	August	Sea	Post-border	Shipping container (household effects)	34	N	Alive	Gold Coast	Gold Coast-Lamington NP
LDN40	Auckland	Oct	Air	Border	Personal effects	35	Y	Alive	Sydney?	Brisbane (sth)
LDN47	Tauranga	April	Air	Post-border	Personal effects	26	N	Alive	Caboolture	Brisbane (nth)
LDN57	Christchurch	April	Air	Post-border	Personal effects	32	N	Alive	Brisbane	Brisbane (sth)
LDN62	Christchurch	August	Sea	Border	Shipping container (household effects)	40	Y	Dead	Brisbane (Kingston)	Gold Coast-Lamington NP
LDN64	Christchurch	Oct	Sea	Border	Shipping container (household effects)	37	Y	Alive	Brisbane (Samford)	Brisbane (nth)
LDN218	Auckland	Dec	Air	Post-border	Personal effects	36	Y	Alive	Unknown	Sydney
LDN230	Wellington	May	Sea	Border	Shipping container (mixed freight)	36	Y	Alive	Sydney	Sydney
LDN231	Invercargill	June	Air	Post-border	Personal effects	35	Y	Alive	Sydney	Nth NSW coast-Port Macquarie

The inferred Australian origin of each specimen from the molecular data is compared to the predicted origin recorded in the Ministry for Primary Industries interception database. All intercepted lizards were found alone rather than in groups. Reproduced with permission from Chapple et al. (2013b)

Table 13.2 Details of the plague skink (*Lampropholis delicata*) specimens intercepted being accidentally transported within New Zealand to regions beyond the established range

	Interception					Lizard			
Sample code	Location	Month	Transport method	Cargo type	Cargo contents	SVL	Adult?	Alive?	Predicted origin
LDN05	Palmerston North	Feb	Truck	Freight	Pet food	40	Y	Dead	Auckland
LDN11	Havelock North	Aug	Truck	Freight	Building materials	39	Y	Dead	Auckland
LDN12	Dunedin	Aug	Truck or trail	Freight	Timber	35	Y	Alive	Auckland
LDN16	Palmerston North	Oct	Truck	Freight	Machinery	40	Y	Alive	Unknown
LDN17	Christchurch	Oct	Truck or trail	Freight	Steel	49	Y	Alive	Auckland
LDN18	Christchurch	Dec	Truck	Freight	Decorations	28	N	Dead	Waihi Beach
LDN22	Christchurch	May	Rail	Container	Mixed freight	33	N	Alive	Auckland
LDN24	Nelson	June	Sea	Shipping container	Household effects	44	Y	Alive	Auckland
LDN29	Palmerston North	Oct	Truck	Courier	Computer	37	Y	Alive	Auckland
LDN30	Palmerston Nth	Oct	Truck	Freight	Engine parts	30	N	Alive	Auckland
LDN33	Christchurch	May	Sea	Shipping container	Beverages	40	Y	Alive	Auckland
LDN37	Christchurch	July	Truck	Freight	Electrical fittings	39	Y	Alive	Auckland
LDN45	Palmerston North	Feb	Truck	Freight	Building materials	38	Y	Alive	Auckland
LDN49	Palmerston North	May	Truck	Freight	Pipe fittings	36	Y	Alive	Auckland
LDN51	Porirua	July	Truck	Freight	Vegetables	22	N	Alive	Auckland
LDN58	New Plymouth	May	Truck	Freight	New car	37	Y	Alive	Auckland
LDN61	Christchurch	June	Rail or sea	Container	Unknown	38	Y	Alive	Auckland
LDN68	Napier	March	Truck	Freight	Plasticware	14	N	Dead	Auckland
LDN217	Dunedin	Nov	Truck	Freight	Mail	30	N	Alive	Unknown
LDN219	Napier	Dec	Truck	Freight	Mail	27	N	Alive	Auckland
LDN223	Palmerston North	Oct	Unknown	Unknown	Unknown	34	N	Alive	Unknown
LDN224	Stratford	Oct	Truck	Freight	Ceramics	26	N	Alive	Auckland

LDN225	Rotorua	Nov	Truck	Freight	Beverages	39	Y	Dead	Auckland
LDN232	New Plymouth	July	Truck	Freight	Steel	40	Y	Alive	Auckland

All intercepted lizards were found alone rather than in groups. Note that the plague skink did not establish in Palmerston North until ~2007. Reproduced with permission from Chapple et al. (2013b) on Great Barrier Island (GBI) is currently the focus of containment, with a view to eradicate plague skinks from the island altogether (Wairepo 2015).

13.3 Ecology, Life History and Reproduction in New Zealand

Previous species introductions to New Zealand indicate that even the basic ecology of a species may change markedly outside its native environment (e.g. Fitzgerald 1984; Green 1984). However, there are no striking differences in the life history of plague skinks in New Zealand compared to other regions across their native and introduced range (Table 13.3), although Lord Howe Island females tend to have a larger body size, and Sydney males are smaller than those from New Zealand.

There is marked sexual dimorphism in the plague skink, both in New Zealand and in its native Australian range, with females having larger SVL and interlimb length (ILL) and males having longer and broader heads (DGC unpublished data). Sexual dimorphism in these traits has also been documented on Lord Howe Island (Chapple et al. 2014). Similarly, in Massey, Auckland, female body size is larger than that of males (JEP unpublished data). Male body size also varies between populations, with the densest populations consisting of the smallest individuals (Peace 2004; JEP unpublished data; Table 13.3).

Plague skinks have tail lengths that average 155 % of the mean adult SVL. Overall, 59 % of plague skinks around Auckland have broken or regenerating tails, and whilst no differences are evident between populations or sexes, the proportion of individuals with tail loss varies among age groups. Juveniles have the lowest percentage of tail loss (22 %), an intermediate level of tail loss occurs in subadults (49 %), and adults display the highest incidence of tail loss (72 %) (Peace 2004; JEP unpublished data). Plague skinks also frequently lose their toes, with Peace (2004) reporting toe loss in 31 % of plague skinks. The proportion of individuals missing toes differed significantly between populations, and there was a positive trend towards toe loss in larger individuals (Peace 2004). No significant sexual differences in toe loss were evident (Peace 2004). Tail and toe loss in lizards is frequently attributed to predation (e.g. Whitaker 1968; Qualls and Shine 1998; Hare and Miller 2010); the observed trends may be due to the higher conspicuousness of adults to predators as a result of body size or longer movements, or could be a function of time, with older individuals exposed to predation and intraspecific aggression for a greater period of time (Peace 2004). Additionally, toe loss may occur due to dysecdysis (incomplete sloughing) (Frye 1981; Gartrell 2016). Percentages of tail and toe loss are comparable to those recorded for native New Zealand lizard populations and for plague skink populations in Australia and Lord Howe Island (Forsman and Shine 1995; Hare and Miller 2010; Chapple et al. 2014).

Plague skinks are oviparous, and eggs of New Zealand populations hatch in February and March (Gill and Whitaker 2001). Nests occur in a range of sheltered

Table 13.3 Comparative life history of the plague skink (*Lampropholis delicata*) across its native Australian range and introduced range (Hawaiian Islands, New Zealand, Lord Howe Island [LHI])

Country	Location (Latitude)	Female body size (mm)		Male body size (mm)		Clutch size		Size at maturity (mm)	Hatchling size (mm)
		Mean ± SE (*n*)	Range	Mean ± SE (*n*)	Range	Mean ± SE (*n*)	Range		
Australia	Townsville (20 °S)[a]	37.8 ± 2.35 (44)	NA	36.9 ± 1.86 (44)	NA	3.0 ± 0.84 (21)	1–4	35	21
	Brisbane (27 °S)[a]	38.8 ± 2.96 (39)	NA	38.7 ± 2.65 (67)	NA	3.1 ± 0.88 (22)	2–5	35	16
	Coffs Harbour (31 °S)[a]	37.5 ± 4.11 (64)	NA	36.5 ± 3.64 (53)	NA	3.7 ± 1.31 (22)	2–8	31	15
	Sydney (34 °S)[a]	37.0 ± 2.99 (69)	NA	36.1 ± 2.39 (102)	NA	3.1 ± 1.07 (14)	2–6	32	16
	Melbourne (37 °S)[a]	39.6 ± 3.78 (73)	NA	39.9 ± 3.84 (48)	NA	4.4 ± 2.03 (19)	1–8	33	17
	Tasmania (41 °S)[a]	39.6 ± 3.78 (73)	NA	39.9 ± 3.84 (48)	NA	4.4 ± 2.03 (19)	1–8	33	17
Hawaii	Oahu (21 °N)[a]	38.7 ± 1.59 (26)	NA	38.3 ± 1.72 (26)	NA	3.1 ± 1.22 (23)	1–5	36	17
	Oahu (21 °N)[b]	38.6 ± 1.7 (45)[c]	NA	NA	NA	3.5 ± 1.8 (45)	1–5	NA	NA
	Kauai (22 °N)[b]	41.8 ± 3.5 (9)[c]	NA	NA	NA	4.1 ± 1.0 (9)	3–6	NA	NA
	Hawaii (19 °N)[b]	41.2 ± 2.8 (10)[c]	NA	NA	NA	4.7 ± 1.3 (10)	3–7	NA	NA
	All islands (19–22 °N)[d]	40.6 ± 0.3 (143)[c]	35–47	39.5 ± 0.2 (159)[c]	35–46	4.0 ± 0.13 (106)	1–7	31	NA
LHI	Lord Howe Island (31 °S)[e]	44.4 ± 0.25 (349)[c]	35–57	42.8 ± 0.20 (367)[c]	35–55	3.4 ± 0.13 (63)	1–7	33–35	NA

(continued)

Table 13.3 (continued)

Country	Location (Latitude)	Female body size (mm)		Male body size (mm)		Clutch size		Size at maturity (mm)	Hatchling size (mm)
		Mean ± SE (*n*)	Range	Mean ± SE (*n*)	Range	Mean ± SE (*n*)	Range		
New Zealand	North Island (36–37 °S)[d]	40.8 ± 0.60 (39)[c]	35–51	40.0 ± 0.38 (52)[c]	35–46	4.1 ± 0.40 (7)	3–6	41	NA
	Great Barrier Island (36 °S)[f]	41.5 ± 3.9 (31)[c]	NA	NA	NA	3.6 ± 1.1 (31)	NA	NA	NA
	Motutapu Island (36 °S)[g]	41.9 ± 1.17 (9)[c]	36–46	38.4 ± 1.04 (7)[c]	36–44	NA	NA	35	17
	Rangitoto Island (36 °S)[g]	39.5 ± 0.46 (31)[c]	36–46	39.6 ± 0.55 (15)[c]	37–43	NA	NA	34	12
	Massey, Auckland (36 °S)[g]	40.2 ± 0.82 (55)[c]	36–46	38.7 ± 0.79 (51)[c]	36–42	4.7 ± 1.37 (3)	4–5	32	16
	Avondale, Auckland (36 °S)[g]	40.6 ± 1.16 (37)[c]	36–46	40.2 ± 1.36 (41)[c]	36–44	5.0 ± 2.16 (2)	4–6	31	15
	Otara, Auckland (36 °S)[g]	40.3 ± 0.81 (58)[c]	36–48	40.3 ± 1.00 (42)[c]	36–44	4.7 ± 0.52 (7)	3–7	30	17

[a] Forsman and Shine (1995)
[b] Baker (1979)
[c] Restricted analysis to adults
[d] DGC unpublished data
[e] Chapple et al. (2014)
[f] Wairepo (2015)
[g] Peace (2004), JEP unpublished data

microhabitats including cavities in banks, under rocks and in leaf litter (Peace 2004). This type of egg placement has often been observed in species that do not burrow well (Shine 1985). In the Auckland region, the mean clutch size is 4.75 (±0.33, $n = 12$, range 3–7), which is slightly greater than for the Great Barrier and Lord Howe Island populations (GB: 3.58 ± 1.1, $n = 31$; LH 3.4, range 1–7) (Peace 2004; Chapple et al. 2014; Wairepo 2015). Larger females tend to have larger clutch sizes (Baker 1979; Shine 1983; Peace 2004; Chapple et al. 2014). Eggs are laid in communal nests around Auckland from December to April (3–30+ eggs), with communal nesting also observed on the Coromandel Peninsula, on Rangitoto Island (40+ eggs) (Peace 2004; Peace 2011; DGC pers obs) and also on Lord Howe Island (11–200+ eggs; Chapple et al. 2014).

Auckland populations display an equal sex ratio, and testis and ovary volumes track the same seasonal fluctuations among sites (Peace 2004). Testis volume is low during September and October, increasing in November, reaching maximum volume in February and then decreasing through March and April. Enlarged ova are present from September onwards with the earliest yolked ova detected in February and the latest in March. Egg follicles are smallest from February to April and markedly larger in diameter between September and October (Peace 2004). In comparison, Lord Howe Island populations are reproductively active from September to February (Chapple et al. 2014). Most aspects of the reproductive biology of plague skinks in New Zealand (mean clutch size and general testis and ovary condition) are very similar to those in Australia and Hawaii (Baker 1979; Shine 1983; Joss and Minard 1985; Forsman and Shine 1995).

In New Zealand, plague skinks utilise a variety of habitats, ranging from highly modified environments (glasshouses, nurseries and well-maintained gardens) to shrubland (irregularly maintained, revegetated sites) and rank vegetation (weedy areas beside roadsides, railway sidings and industrial sites). On Rangitoto Island, they occupy lava formations from the supralittoral zone to the summit (Gill and Whitaker 2001; Peace 2004, 2011). A variety of refuges, including leaf litter, fallen logs, shade cloth and glass bottles, are used by most individuals (88 %), with these often occurring under a canopy (56 %) (Peace 2004). Plague skinks are diurnal, and in New Zealand, the peak in seasonal activity occurs from November to December (Peace 2004). Captive individuals are most often observed basking, although foraging activity is also frequent (Peace 2004). Plague skinks feed opportunistically on invertebrates (Wilson and Swan 2013; Cogger 2014), although there have been no detailed investigations of their diet in New Zealand. Vision and olfaction are used to search for prey items in leaf litter and refuges. Prey items are rapidly pursued when disturbed and are often caught with a quick lunge. Foraging lizards crowd around each other and attempt to catch invertebrates disturbed by other animals. Those that have captured prey are often pursued and bitten by conspecifics in an attempt to take prey from their mouths, both in the wild and captivity (Peace 2004).

13.4 Potential Impact of the Plague Skink in New Zealand

When plague skinks initially established in New Zealand, they were regarded as a protected species under the New Zealand Wildlife Act 1953; this status lasted until 2010, when they were included in Schedule 5 (‘wildlife not protected’) of the Wildlife Act and simultaneously listed as an ‘unwanted organism’ under the Biosecurity Act 1993. Plague skinks and native New Zealand lizards overlap widely in terms of geographic distribution and habitat use (Chapple and Hitchmough 2016), occurring sympatrically in many locations. When compared with native species, the more delicate form of plague skinks would confer considerable advantages in the introduced species; it would allow smaller refuges to be utilised and assist tail shedding and predator escape, thereby increasing its survival relative to native species in the presence of introduced predators, such as rodents (Peace 2004). Plague skinks arriving into New Zealand from Australia may also introduce parasites since exotic lizards intercepted entering New Zealand carry a range of ectoparasites, mostly mites (Heath and Whitaker 2015; Gartrell 2016). Mites hosted by plague skinks could impact the native herpetofauna directly or through vectoring diseases (e.g. Goka et al. 2013; Gartrell 2016).

Plague skinks occur in sympatry with native New Zealand lizards throughout large parts of their range. They are generalist feeders that forage for the same invertebrate prey (size and type) as the native New Zealand copper skink (*Oligosoma aeneum*) using similar foraging tactics (Peace 2004), suggesting that the two species compete for prey resources. Nonetheless, in captive populations, body condition indices for copper and plague skinks housed communally and, separately, do not differ within species over time (Peace 2004), though plague skinks are always more abundant in areas of sympatry with native lizard species in the Auckland region (e.g. three copper skinks versus 194 plague skinks; Peace 2004). No interspecific interactions have been observed in the field or captivity, and individuals of each species do not appear to avoid each other spatially (Peace 2004). Plague skinks have a larger clutch size than copper skinks and therefore have a higher potential annual reproductive output (Shine 1983; Joss and Minard 1985; Forsman and Shine 1995; Peace 2004; Cree and Hare 2016; Table 13.3). The difference in abundance observed for sympatric Auckland populations may reflect the hardiness of plague skinks to predation and habitat disturbance, as well as their greater reproductive output. This apparent increase in plague skink numbers may artificially elevate the abundance of predatory species, which in turn may result in greater predation pressure on native lizards (Norbury 2001).

Moth skinks (*Lipinia noctua*) and *Emoia impar* appear to have been replaced by the rapidly expanding populations of plague skinks in the Hawaiian Islands (Hunsaker and Breese 1967; Baker 1979), but the evidence for this is currently circumstantial (Fisher and Ineich 2012). On Lord Howe Island, the plague skink has the potential to impact the island’s endemic invertebrate fauna (Chapple et al. 2014), although, again, the evidence is anecdotal. Thus, at present, there is no conclusive data for the negative impact of plague skink in New Zealand or elsewhere in its invasive range.

13.5 Stopping the Spread of the Plague Skink in New Zealand

Whilst the plague skink has spread across much of New Zealand's North Island, during the past five decades, their establishment on inshore and offshore islands has been limited to Rangitoto-Motutapu and Waiheke Islands in the Hauraki Gulf. In recent years, however, they have expanded their range. They have colonised and established on Rotorua and Kawau Islands, all inshore islands in the Hauraki Gulf, continue to be occasionally intercepted in the South Island and have been detected in a timber shipment arriving on Raoul Island in the Kermadec island group, which lacks any indigenous terrestrial reptiles (Fisher 2011). Plague skinks were first detected on GBI in April 2013 during a presence/absence survey conducted by Auckland Council, and their establishment on GBI represents the first incursion of a breeding population of plague skinks on a New Zealand offshore island (Wairepo 2013). The discovery elicited a biosecurity response led by Auckland Council. GBI is a valuable ecological asset since it is free of mustelids, hedgehogs (*Erinaceus europaeus*), Norway rats (*Rattus norvegicus*), deer (Cervidae) and brush-tailed possums (*Trichosurus vulpecula*). Of equal concern was for the potential for plague skinks to reach other, more pristine and important conservation islands in the outer Gulf and beyond.

The response to this incursion highlighted the paucity of knowledge and tools to attempt either containment or eradication for small lizards. Whilst the skinks remained restricted to the vicinity of the Tryphena Wharf, ascertained using tracking tunnel monitoring at potential incursion sites across the island (Wairepo 2013), a programme of trapping was instigated using insect sticky traps (Wairepo 2015; see Lettink and Hare 2016). Insect sticky traps were used in place of conventional methods, such as pitfall trapping, due to perceived logistical challenges of establishing pitfall trapping grids and the ability to rapidly set up sticky traps (see Lettink and Hare 2016). These were deployed in an area greater than the incursion area and at higher densities than standard traps. Funnel trapping (see Lettink and Hare 2016) was attempted as a supporting technique on steep terrain. Whilst initial insect sticky traps capture rates looked promising, lizard removal rates did not result in a declining capture rate over the period of the study, and it was not possible to identify differences in capture probabilities between insect sticky traps and funnel traps (Wairepo 2015). Drift fencing was also recommended for the delimitation of the incursion, but these were only placed along small sections due to financial constraints.

These results suggest that plague skinks cannot be easily eradicated with modest density trapping of the incursion area and further support the recommendation that the efficacy of a number of interception methods need to be evaluated at a range of device and skink densities in order to determine their potential role as eradication tools. Without this research, it remains likely that plague skinks will continue to expand, both through natural dispersion and via human-mediated incursion pathways, to new habitats that can sustain them.

Research into the toxicant, acetaminophen, as a potential control or eradication tool for the plague skink has also been conducted (Wairepo 2015). Whilst acetaminophen is acutely toxic to plague skinks at an appropriate dosage, non-target risks and the need to develop effective means for field delivery currently prevent its development for operational use.

In the absence of eradication methods, containing the spread of plague skinks relies entirely on biosecurity measures. The Auckland Council, in partnership with other government and conservation agencies, has established a ‘Treasure Island’ initiative, which aims to increase awareness of invasion pathways and the role of biosecurity to minimise the risks of pest species being transported on vessels or in freight (http://treasureislands.co.nz/). This work includes the use of detector dogs (see Lettink and Hare 2016), which, together with their handlers, are able to communicate the biosecurity message whilst also detecting plague skinks. There is still a serious shortage of biosecurity tools to assist in the effective quarantining of materials originating from mainland locations occupied by plague skinks. A recent biosecurity advancement that may contribute to quarantine measures for plague skinks is the use of thermal fumigants. These involve the application of hot air (48–52 °C) at 3.4 m^3/min and have been used to prompt the invasive brown tree snake (*Boiga irregularis*) to become active so that they are more easily detected (Kraus et al. 2015). Such a treatment of cargo is easily achieved using conventional heaters and containment measures and, if adapted for small skinks, might provide a valuable tool to improve detection of plague skinks. However, the primary constraint of biosecurity measures for plague skinks remains the detection and destruction of their eggs. Plague skinks frequently deposit their eggs in disturbed surface soils, including the soil of potted plants, making the movement of horticultural products a high-risk invasion pathway (Baker 1979; see above). Currently the only robust measure to combat this risk is to de-soil plant roots prior to transport.

Plague skinks have, as yet, failed to establish on the South Island of New Zealand (see Sect. 13.2), despite the potential suitability of the climate and habitat through the northeast of the South Island and the lack of biosecurity barriers to freight, transport and trade between the islands. Given the failure to contain and eradicate the plague skink incursion on GBI and the high conservation values of the offshore island reserves of New Zealand’s South Island, the development of effective detection and removal methods for this invasive species is a biosecurity research priority. Eradication of a recent incursion of this species is likely to depend equally on available eradication tools and the sensitivity of monitoring to detect an incursion early in their establishment phase. This challenge is complicated by the nature of human-mediated ‘jump dispersal’, which is the common mode of spread in plague skinks within New Zealand (Chapple et al. 2013b).

Acknowledgements We thank D. Brunton, B. Gill, A. Polkanov, N. Schumann, M. Thompson, R. Tingley, G. Ussher and A.H. Whitaker for advice and assistance. Our plague skink research has been funded by the Australian Research Council (grant to DGC; DP0771913), the National Geographic Society (grant to DGC; 8085-06, 8952-11), the Hermon Slade Foundation (grant to DGC; HSF 09-02), the Allan Wilson Centre for Molecular Ecology and Evolution (to DGC), the Monash University School of Biological Sciences Small Grant (to DGC), Auckland Council (to JEP), Bart Baker Memorial Scholarship in Vertebrate Pest Management (to JEP), James Sharon Watson Conservation Trust (to JEP) and the University of Auckland (to JEP).

References

Baker JK (1979) The rainbow skink, *Lampropholis delicata*, in Hawaii. Pac Sci 33:207–212

Chaplin K (2013) Intra-specific hybridisation of the delicate skink (*Lampropholis delicata*) on Lord Howe Island. Honours thesis, School of Biological Sciences, Monash University

Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Thompson MB (2009) Isolation and characterization of microsatellite loci from the invasive delicate skink (*Lampropholis delicata*), with cross-amplification in other Australian *Eugongylus* group species. Conserv Genet Resour 1:55–58

Chapple DG, Hoskin CJ, Chapple SNJ, Thompson MB (2011a) Phylogeographic divergence in the widespread delicate skink (*Lampropholis delicata*) corresponds to dry habitat barriers in eastern Australia. BMC Evol Biol 11:191

Chapple DG, Simmonds SM, Wong BBM (2011b) Know when to run, know when to hide: can behavioral differences explain the divergent invasion success of two sympatric lizards? Ecol Evol 1:278–289

Chapple DG, Chapple SNJ, Thompson MB (2011c) Biogeographic barriers in south-eastern Australia drive phylogeographic divergence in the garden skink, *Lampropholis guichenoti*. J Biogeogr 38:1761–1775

Chapple DG, Simmonds SM, Wong BBM (2012) Can behavioral and personality traits influence the success of unintentional species introductions? Trends Ecol Evol 27:57–64

Chapple DG, Miller KA, Kraus F, Thompson MB (2013a) Divergent introduction histories among invasive populations of the delicate skink (*Lampropholis delicata*): has the importance of genetic admixture in the success of biological invasions been overemphasized? Divers Distrib 19:134–146

Chapple DG, Whitaker AH, Chapple SNJ, Miller KA, Thompson MB (2013b) Biosecurity interceptions of an invasive lizard: origin of stowaways and human-assisted spread within New Zealand. Evol Appl 6:324–339

Chapple DG, Miller KA, Chaplin K, Barnett L, Thompson MB, Bray RD (2014) Biology of the invasive delicate skink (*Lampropholis delicata*) on Lord Howe Island. Aust J Zool 62:498–506

Chapple DG, Knegtmans J, Kikillus H, van Winkel D (2016) Biosecurity of exotic reptiles and amphibians in New Zealand: building upon Tony Whitaker's legacy. J R Soc N Z 46:66–84

Cheetham E, Doody JS, Stewart B, Harlow P (2011) Embryonic mortality as a cost of communal nesting in the delicate skink. J Zool 284:234–242

Cogger HG (2014) Reptiles and amphibians of Australia, 7th edn. CSIRO Publishing, Melbourne, VIC

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Cromie GL, Chapple DG (2012) Impact of tail loss on the behaviour and locomotor performance of two sympatric *Lampropholis* skink species. PLoS One 7, e34732

Doody JS, Paull P (2013) Hitting the ground running: environmentally cued hatching in a lizard. Copeia 2013:160–165

Fisher NR (2011) Considering native and exotic terrestrial reptiles in island invasive species eradication programmes in the Tropical Pacific. In: Veitch CR, Clout MN, Towns DR (eds) Island invasives: eradication and management. IUCN, Gland, pp 51–55

Fisher R, Ineich I (2012) Cryptic extinction of a common Pacific lizard *Emoia impar* (Squamata, Scincidae) from the Hawaiian Islands. Oryx 46:187–195

Fitzgerald AE (1984) Diet of the possum (*Trichosurus vulpecula*) in three Tasmanian forest types and its relevance to the diet of possums in New Zealand forests. In: Smith A, Hume I (eds) Possums and gliders. Surrey Beatty & Sons, Chipping Norton, NSW, pp 137–143

Forsman A, Shine R (1995) Parallel geographic variation in body shape and reproductive life history within the Australian scincid lizard *Lampropholis delicata*. Funct Ecol 9:818–828

Frye FL (1981) Traumatic and physical diseases. In: Cooper JE, Jackson OF (eds) Diseases of the Reptilia, vol 2. Academic, London, pp 387–407

Gartrell B (2016) Diseases of New Zealand reptiles. Chap. 8. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Gill B, Whitaker T (2001) New Zealand frogs and reptiles. David Bateman, Auckland

Goka K, Okabe K, Takano A (2013) Recent cases of invasive alien mites and ticks in Japan: why is a regulatory framework needed? Exp Appl Acarol 59:245–261

Green WQ (1984) A review of ecological studies relevant to management of the common brushtailed possum. In: Smith A, Hume I (eds) Possums and gliders. Surrey Beatty & Sons, Chipping Norton, NSW, pp 483–499

Greer AE (1989) The biology and evolution of Australian lizards. Surrey Beatty & Sons, Sydney, NSW

Hare KM, Miller KA (2010) Frequency of tail loss does not reflect innate predisposition in temperate New Zealand lizards. Naturwissenschaften 97:197–203

Heath A, Whitaker AH (2015) Mites (Acari: Pterygosomatidae, Macronyssidae) taken from lizards intercepted at the New Zealand border. Syst Appl Acarol 20:739–756

Hitchmough R, Barr B, Monks J, Lettink M, Reardon J, Tocher M, van Winkel D, Rolfe J (2016a) Conservation status of New Zealand reptiles, 2016, New Zealand threat classification series 2. Department of Conservation, Wellington

Hitchmough RA, Patterson GB, Chapple DG (2016b) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hunsaker D, Breese P (1967) Herpetofauna of the Hawaiian Islands. Pac Sci 21:423–430

Hutchinson MN, Thompson MB, Stewart JR (2005) *Lampropholis delicata* (Delicate skink, Rainbow skink). Introduction. Herpetol Rev 36:450–451

Joss JMP, Minard JA (1985) On the reproductive cycles of *Lampropholis guichenoti* and *L. delicata* (Squamata: Scincidae) in the Sydney region. Aust J Zool 33:699–704

Kraus F (2009) Alien reptiles and amphibians. Springer, Cham

Kraus F (2015) Impacts from invasive reptiles and amphibians. Annu Rev Ecol Evol Syst 46:75–97

Kraus F, Stahl R, Pitt W (2015) Thermal fumigation provides a simple and effective solution for sanitizing cargo from invasive snakes. J Pest Sci 88:331–341

Lettink M, Hare KM (2016) Sampling techniques for New Zealand lizards. Chap. 10. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Lever C (2003) Naturalized reptiles and amphibians of the world. Oxford University Press, Oxford

Michelangeli M, Wong BBM, Chapple DG (2016) It's a trap: sampling bias due to animal personality is not always inevitable. Behav Ecol 27:62–67

Moule H, Chaplin K, Bray RD, Miller KA, Thompson MB, Chapple DG (2015) A matter of time: temporal variation in the introduction history and population genetic structuring of an invasive lizard. Curr Zool 61:456–464

Moule H, Michelangeli M, Thompson MB, Chapple DG (2016) The influence of urbanization on the behaviour of an Australian lizard, and the presence of an activity-exploratory behaviour syndrome. J Zool 298:103–111

New Zealand Herpetofauna database (2015). http://www.doc.govt.nz/conservation/native-animals/reptiles-and-frogs/reptiles-and-frogs-distribution-information/electronic-atlas/

Norbury G (2001) Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. J Appl Ecol 38:1350–1361

Peace JE (2004) Distribution, habitat use, breeding and behavioural ecology of rainbow skinks (*Lampropholis delicata*) in New Zealand. Masters thesis, University of Auckland

Peace JE (2011) Annual reptile survey of Rangitoto and Motutapu Islands (2011). Report DOCDM-752499, Department of Conservation, New Zealand

Qualls CP, Shine R (1998) *Lerista bougainvillii*, a case study for the evolution of viviparity in reptiles. J Evol Biol 11:63–78

Schulz M (2009) Notes on the delicate skink *Lampropholis delicata* occurring on Lord Howe Island. Herpetofauna 39:48–52

Shine R (1983) Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. Oecologia 57:397–405

Shine R (1985) The reproductive biology of Australian reptiles: a search for general patterns. In: Grigg G, Shine R, Ehmann H (eds) Biology of Australasian frogs and reptiles. Surrey Beatty & Sons, Chipping Norton, NSW, pp 297–303

Tingley R, Hitchmough RA, Chapple DG (2013) Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol Conserv 165:62–68

Tingley R, Thompson MB, Hartley S, Chapple DG (2016) Patterns of niche filling and expansion across the invaded ranges of an Australian lizard. Ecography 39:270–280

Towns DR, Perrott J, Hitchmough RA (2016) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Toy SJ, Newfield MJ (2010) The accidental introduction of invasive animals as hitchhikers through inanimate pathways: a New Zealand perspective. Rev Sci Tech 29:123–133

Wairepo J (2013) Presence absence survey to detect rainbow skinks on Great Barrier Island. Unpublished report to Auckland Council

Wairepo J (2015) Developing biosecurity strategies for an invasive reptile, the plague skink (*Lampropholis delicata*) on Great Barrier Island. MSc thesis, Massey University, Auckland

Whitaker AH (1968) The lizards of the Poor Knights Islands, New Zealand. N Z J Sci 11:623–651

Wilson S, Swan G (2013) A complete guide to reptiles of Australia, 4th edn. Reed New Holland, Sydney, NSW

Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends Ecol Evol 24:136–144

Chapter 14
The Future of New Zealand Lizard Research

David G. Chapple

Abstract This book provides the first detailed synthesis of the history, fossil record, taxonomy, biogeography, ecology, diseases, physiology, sampling methods, life history, and reproduction and conservation of the New Zealand lizard fauna. In collating our current knowledge of New Zealand lizards, it has been possible to critically assess the lizard research that has been conducted on New Zealand species. Conservation, the development of sampling and monitoring methods, and the pioneering ecological studies conducted in the 1950s–1970s represent the clear strengths of this research. In contrast, the main areas of deficiency relate to a failure to publish research findings, a narrow focus on conservation-related research, a slow rate of species description, and a limited awareness of the value of natural history collections. To rectify these weaknesses, several priority research directions are outlined. These include (1) comparative osteological studies; (2) taxonomic research; (3) biogeographic studies; (4) detailed investigations of ecology, physiology, reproduction, and life history; (5) research into how lizard populations persist on the main islands in the presence of mammalian predators; (6) quantitative studies examining the value of mainland conservation sanctuaries; and (7) quantification of the impact of the plague skink on the native New Zealand biota.

Keywords Biogeography • Conservation • Disease • Ecology • Fossil record • Gecko • Life history • Physiology • Reproduction • Sampling methods • Skink • Species discovery • Taxonomy

14.1 Our Current Knowledge of the New Zealand Lizard Fauna

This book represents the first comprehensive synthesis of the New Zealand lizard fauna and outlines the current state of our knowledge of its history, fossil record, taxonomy, biogeography, ecology, life history and reproduction, diseases,

---

D.G. Chapple (✉)
School of Biological Sciences, Monash University, 25 Rainforest Walk, Clayton, VIC 3800, Australia
e-mail: David.Chapple@monash.edu

D.G. Chapple (ed.), *New Zealand Lizards*, DOI 10.1007/978-3-319-41674-8_14

physiology, sampling methods, and conservation. Here I summarise the key aspects of each chapter, provide a critical assessment of the strengths and weaknesses of lizard research in New Zealand, and outline several priority areas for future research.

Shea (2016) outlined that discovery of lizard species in New Zealand began with Māori in the thirteenth century and continues through to today. A key moment in the history of New Zealand lizard research was the transition from European-based scientists (who were predominant during the 1800s) to the locally based researchers who have progressed our knowledge of the fauna since the 1950s. As knowledge of the New Zealand lizards increased in the 1970s, upsurge in the number of field-based ecological studies occurred. Similarly, the rise of the molecular age in the 1980s was accompanied by a large spike in taxonomic activity and species description, a trend that has continued (albeit slowly) through to the present day. Interestingly, different authors in the book hold divergent views as to the origin of the world's largest known gecko, the kawekaweau, or *Hoplodactylus delcourti*. Shea (2016) concludes that it is a New Zealand species, whereas Worthy (2016) argues that, due to the lack of fossil material, it most likely originates from elsewhere in the Pacific (e.g. New Caledonia). Ancient DNA methods may hold the key to solving the mystery of the origin of this enigmatic specimen.

Worthy (2016) provided the first detailed review of the available fossil material for New Zealand lizards. The oldest known fossil deposit containing lizards is from the Miocene (19-16 mya; St Bathans Fauna), with representatives of both extant lineages present (diplodactylid geckos and Eugongylinae skinks). There is then a large gap in the lizard fossil record until the quaternary (within the last 50,000 years). The quaternary fossil record provides us with a glimpse of the diversity and distribution of lizards prior to the arrival of humans. However, this record is biased towards large-bodied species, and our ability to interpret it is hindered by the limited comparative osteological material held in museums for extant species. Thus, it is currently difficult to confidently assign fossil material to, or distinguish from, currently recognised species.

In Chap. 4, Hitchmough et al. (2016a) discussed how a wealth of recent taxonomic activity and new species descriptions, driven by molecular studies, has resulted in a near trebling of the known extant lizard fauna in New Zealand (from 38 in the 1980s to 104 at last count). This massive increase in species discovery is due to both the splitting of previously widespread, single species into multiple taxa (i.e. the identification of cryptic taxa) and the discovery of new taxa, generally in remote regions of the country. Unfortunately, the rate of species description has not kept pace with the accelerated rate of species discovery, and almost half (45 %) of all recognised lizard species remain to be formally described. All native skinks in New Zealand are currently assigned to *Oligosoma*, with eight main genetic clades within the genus. The relationships among clades are poorly resolved, and no reliable characters have been identified to distinguish among each genetic clade. Taxonomic work is currently in progress to formally describe the ~22 undescribed taxa (G.B. Patterson and S. Melzer, unpublished data; B. Barr, R. Hitchmough, D.G. Chapple, unpublished data). Seven gecko genera are recognised in

New Zealand, with each readily diagnosable. A taxonomic monograph is currently in preparation, which will formally describe the majority of the ~25 undescribed gecko taxa in New Zealand (R.A. Hitchmough, S.V. Neilsen, A. Bauer, unpublished data).

Geckos colonised New Zealand during the Eocene-Oligocene, well before the skinks, which arrived in the country during the Miocene. In Chap. 5, Chapple and Hitchmough (2016) highlighted how previous studies of the processes that have influenced the biogeographic patterns of New Zealand lizards have been hampered by post-human range contractions and extinctions, as well as by a limited grasp on the true diversity of the native fauna. However, improved knowledge of the quaternary lizard fossil record (Worthy 2016) and species boundaries and distributions (Hitchmough et al. 2016a) has allowed more detailed biogeographic analyses to be conducted. Key historical processes that have been identified include (1) sea level changes during the Pliocene-Pleistocene in northern New Zealand, (2) the Pliocene marine inundation of the lower North Island, (3) the impact of water barriers such as Cook Strait (separating the North and South Islands) and Foveaux Strait (separating the South Island and Stewart island), (4) tectonic activity along the Alpine Fault, and (5) regional north–south differentiation within the South Island. In addition, an updated list of 22 biogeographic categories was provided for New Zealand lizards. Interestingly, New Zealand lizards exhibit the signature of allopatric speciation, with minimal overlap in geographic distribution among species within the same genus or clade, but substantial geographic overlap (and widespread sympatry) among species from different clades or genera.

Hare and colleagues (2016) emphasised that detailed information on a range of fundamental ecological traits, such as habitat use, is still lacking for the majority of New Zealand lizard species. Indeed, few detailed, long-term ecological studies have been completed, and the vast majority of our knowledge stems from short-term, or anecdotal, studies. Despite these issues, New Zealand lizards appear to display a range of interesting, or rare, ecological traits. A small number of species are habitat generalists, but most have specific habitat requirements, and high levels of sympatry exist in some environments. Although most skink species are terrestrial, only 30 % of geckos are classed as terrestrial. Many New Zealand lizard species exhibit evidence for strong site fidelity, often over a period of several years. Diet has only been reported for ~40 % of species, with most appearing to be omnivorous. New Zealand lizard species may play a key role in seed dispersal and pollination; such lizard-plant interactions have rarely been reported elsewhere in the world. Temporal niche shifts appear to be widespread in New Zealand lizards. The lizard fauna comprises both nocturnal skinks (7 %; globally, most skinks are diurnal) and diurnal geckos (36 %; geckos are ancestrally nocturnal). The courtship and mating behaviours of native species are poorly known, though sociality, which is rare internationally (Gardner et al. 2016), is present in some New Zealand lizards. A range of avian, mammalian, reptilian, and invertebrate predators of New Zealand lizards have been documented. New Zealand lizards, and particularly geckos, use colour for crypsis and camouflage. Finally, Hare et al. (2016) described vocalisations and defence behaviour in geckos.

Cree and Hare (2016) highlighted that New Zealand lizards are characterised by 'slow' life histories. Many species exhibit low annual reproductive output when compared with similar species overseas, and several gecko species have fewer than two offspring each year (gecko species worldwide are limited to a maximum clutch size of two). However, New Zealand lizard species are generally long-lived, with several species documented to live for as long as 30–50 years, and this may, in part, explain the 'slow' life histories. Probably as a consequence of New Zealand's cold climate, virtually all native lizard species (except *O. suteri*) are viviparous. Temperature also influences gestation length in females, and some species exhibit prolonged pregnancies, where fully developed young are retained in utero over winter (i.e. biennial reproduction). Although it is difficult to determine the sex of juvenile or subadult lizards, sexual dimorphism is common in adults of some species. Where sexual dimorphism is present, males generally have larger heads and females larger body size (snout-vent length). Information on reproduction and life history is essential for effective captive breeding programmes and to assess the vulnerability of species to decline.

Gartrell (2016) provided a detailed overview of the diseases and parasites of native, and captive, reptiles in New Zealand. He summarised the leading causes of mortality and provided a review of the specific diseases that can impact reptiles in New Zealand. This information is not only important to ensure the health of wild populations, but it can assist in the husbandry of captive populations maintained as part of conservation programmes. The chapter also highlights the risks posed by diseases and parasites that are carried by exotic species entering New Zealand and emphasises the need for strong biosecurity protocols (see Heath and Whitaker 2015; Chapple et al. 2016a).

Hare and Cree (2016) examined the thermal and metabolic physiology of New Zealand lizards, providing details of how the lizards may have adapted to cold climates, as well as information that is useful for the conservation of native species. New Zealand lizards maintain lower field body temperatures (no species voluntarily exceeds 34 °C) than lizards elsewhere in the world, with New Zealand species displaying low critical thermal minimums and left-shifted thermal performance curves for sprint speed. As expected, metabolic rate increases with body temperature, and warm daytime temperatures, coupled with active basking in most species, assist lizards to maintain essential physiological functions, including embryonic development and digestion. The nocturnally foraging lizard species, in particular, have physiological adaptations (including low energetic cost of locomotion, but high rates of evaporative water loss) to improve performance at the low temperatures at which they are active. Understanding the thermal biology of lizards is useful for many aspects of the conservation of New Zealand species.

The ability to catch lizards, and identify individuals, is an essential component of virtually all studies on New Zealand lizards. Lettink and Hare (2016) provided an overview of the main methods used to sample lizards: systematic searching, live trapping, and artificial retreats. Given the growing ethical concern over toe clipping as a permanent identification method for lizard studies, the chapter also provided consideration of alternative methods for marking lizards for identification.

However, the chapter also highlighted how toe clipping has allowed long-term marking of individuals (which is important in New Zealand, where there is a predominance of long-lived species) and contributed to our knowledge of species longevity, delayed maturity, biennial reproduction, habitat use, dispersal, and population dynamics. The methods outlined in the chapter will allow effective sampling and study of the entire New Zealand lizard fauna, which is vital for effective conservation management.

Towns and colleagues (2016a) emphasised that 83 % of the New Zealand lizard fauna is currently listed as threatened or at risk. The key drivers of decline are invasive mammals, habitat clearing, and climate change. Case studies were used to examine the effectiveness of conservation management of New Zealand lizard species over the past 30 years. Of the five skink species that have been managed continually over this time, two of them now have improved conservation status; two initially declined, but then improved in response to adaptive management; and the plight of the final species has worsened. Clear evidence that conservation efforts can improve the fate of threatened species exists, particularly for those that inhabit offshore islands. Nelson et al. (2016) examined the potential for lizard conservation within mainland sanctuaries. Although the approach holds promise, as mainland conservation sanctuaries occupy a larger area than all offshore island reserves combined, several issues exist. Again, using a case study approach, it is suggested that low-medium predator control is insufficient to ensure positive conservation outcomes for lizards in unfenced sanctuaries. Whilst the conservation benefits for lizards are greater within fenced sanctuaries, the establishment and maintenance of such reserves is very expensive and yet fails to permanently exclude mice, which may be a significant issue for lizard populations. To date, most research on the role of mainland sanctuaries for lizard conservation has focused on skinks, with comparatively little data available for geckos.

Only one species of exotic lizard, the plague skink (*Lampropholis delicata*), has successfully established and become invasive in New Zealand. Chapple and colleagues (2016b) outlined the first arrival in the mid-1960s, from a single source region in northern New South Wales in eastern Australia. Its subsequent spread across the North Island has been characterised by human-assisted jump dispersal. Bioclimatic modelling indicates that the species has the potential to spread across the majority of the North Island and into the Nelson-Marlborough and Canterbury regions of the South Island. Within New Zealand, the plague skink is a habitat generalist, exhibits sexual dimorphism, lays its eggs communally, and exhibits similar reproductive patterns to its native Australian conspecifics. Recently, the plague skink has spread to several conservation-sensitive offshore islands, and it has the potential to spread to others. Thus, effective management strategies are urgently needed to eradicate and/or mitigate the spread of the species within New Zealand.

14.2 A Critical Assessment of New Zealand Lizard Research

I have been involved with New Zealand herpetology for 12 years and have had numerous conversations with friends and colleagues about how lizard research is conducted in New Zealand. However, as I have been based in Australia for the majority of this time (since mid-2007), I have also had an opportunity to view it from afar (well, at least from across the ditch) and gain a perspective of how lizard research is done in New Zealand relative to elsewhere in the world. Here I outline my opinions about the strengths and weaknesses of New Zealand lizard research. The primary aim of this exercise is to spark constructive discussion among New Zealand lizard researchers and, ultimately, facilitate a reassessment of the way in which herpetological research is conducted in the country.

14.2.1 Strengths

Whilst there are several groups with strong and internationally recognised research programmes in physiology (e.g. Alison Cree, University of Otago) and conservation translocations (Dave Towns, Department of Conservation/Auckland University of Technology; Nicola Nelson, Victoria University of Wellington), here I focus on three areas that represent broader strengths within New Zealand herpetology.

1. Conservation New Zealand lizard researchers have a strong conservation ethos and awareness, a trait that is not as widespread elsewhere in the world. (Indeed, I developed my research interest in conservation biology during my 3 years in New Zealand.) Although the native lizard fauna was only awarded full legislative protection in the 1980s (Towns et al. 2016a), New Zealand has pioneered, and is rightly seen as a world leader in, conservation translocations (reviewed in Towns et al. 2016b) and the use of mainland sanctuaries (reviewed in Nelson et al. 2016). These approaches have supported and enhanced intensive in situ conservation efforts on native lizard species (reviewed in Nelson et al. 2014; Hitchmough et al. 2016b; Towns et al. 2016a). Additionally, an awareness of the factors that drive extinction risk in New Zealand lizards (reviewed in Tingley et al. 2013), coupled with comprehensive and regularly updated threat lists for lizards in New Zealand, by the Department of Conservation (Hitchmough et al. 2016c), is used to prioritise lizard conservation efforts. Importantly, these conservation approaches often involve collaborations with community groups and other conservation organisations.

2. Development of Sampling and Monitoring Methods Given the low abundances of lizards in several locations (e.g. mainland locations with high densities of mammalian predators), as well as their cryptic nature, New Zealand lizard species may be difficult to detect or sample. Thus, researchers in New Zealand have spent considerable time developing new lizard sampling techniques, or modifying existing methods to suit the local species and environment (reviewed in Lettink and Monks 2016; Lettink and Hare 2016). This has provided the techniques required to effectively sample and monitor lizard species across a broad range of habitats and environments.

3. Pioneering Ecological Studies The early ecological studies (e.g. Barwick 1959; Whitaker 1968, 1973; Towns 1975) generated a treasure trove of data and information on the ecology, life history, behaviour, reproduction, and conservation of New Zealand lizards (Bartle 2016). The success of these studies stemmed from their establishment of long-term monitoring sites, allowing them to examine, among other things, seasonal and annual trends, mating behaviour (Barwick 1959), diet (Barwick 1959; Towns 1975), and the impact of invasive mammals (Whitaker 1973). Sadly, such studies are now rare in New Zealand (see Sect. 14.2.2).

14.2.2 Weaknesses

1. Failure to Publish Research ‘If it’s not published, it hasn’t been done’ (Scott Keogh, pers. comm.). This was the adage that was drummed into me by my PhD supervisor. Research that has not been published not only withholds potentially useful information from the scientific community, but also leads to situations where the same (or similar) research is conducted on multiple occasions. However, a large amount of our knowledge of New Zealand lizards is held in unpublished works and is therefore not readily accessible (Chapple 2016). This may be a consequence of the relatively high proportion of New Zealand researchers that are based in government departments or environmental consulting agencies, where publication expectations, pressure, and/or time available to publish their research findings in scientific journals is lower than for university researchers. However, recent years have seen a proliferation in the number of biological sciences journals, thereby increasing the number of options for publishing research on New Zealand lizards. Whilst the abundance of unpublished student theses is an issue worldwide, it acts to accentuate the situation in New Zealand. The formation of online thesis repositories by New Zealand universities has acted to increase the broader accessibility of more recently completed student theses, but inclusion in these repositories requires approval by students, and their studies have not been through the peer-review process.

2. Conservation Focus at the Expense of High-Quality Ecological, Evolutionary, and Physiological Research Given that 83 % of the diverse, native lizard species are listed as threatened or at risk (Towns et al. 2016a; Hitchmough et al. 2016c), it is understandable that New Zealand research has a strong conservation focus. For instance, ~50 % of talks on lizard research at recent Society for Research on Amphibians and Reptiles in New Zealand (SRARNZ; 2011, 2013,

2015) conferences have conservation as their primary focus (compared to ~10 % at recent Australian Society of Herpetologists conferences; 2014–2016). It appears that a widely held attitude exists in New Zealand that if a research project does not have a 'direct' conservation benefit, then it should not be conducted, or at least that it represents lower priority research. This warrants consideration of what exactly 'direct conservation benefit' actually means. As highlighted throughout this book, without a proper understanding of the key aspects of a species' biology, we cannot fully understand the species, thereby restricting our ability to conduct effective conservation-focused research. For example, there needs to be a greater appreciation of the nexus that exists among thermal physiology, endocrinology, reproduction, response to climate change, and conservation.

Increasing our understanding of the ecology, life history, reproduction, and physiology of New Zealand lizards will require the completion of rigorous (i.e. sufficient sample sizes, appropriate controls, standardised survey techniques), well-designed, long-term field studies. In addition, greater emphasis needs to be placed on getting the full benefit out of those lizards that are caught or sampled during these studies, even when the study has a conservation focus. This includes determining the sex of individuals, taking a range of morphometric measurements, collecting a tissue sample for genetic and/or taxonomic studies (see below), documenting the presence of ectoparasites, and marking individuals for subsequent identification (see Lettink and Hare 2016). If such an approach was part of the standard fieldwork protocol for New Zealand studies, it would help to address the numerous knowledge gaps identified by the contributing authors throughout this book and ultimately contribute to conservation efforts.

3. Slow Rate of Species Description and a Departure from the Linnaean System Taxonomy underpins all aspects of biological research as it provides names, diagnoses, and distributions for all species. The published descriptions provide the scientific community with the rationale and supporting data for the recognition of the species. Thus, undescribed species are generally not formally recognised by government agencies and international conservation organisations. For instance, undescribed species are ineligible for conservation listing by the IUCN (2016) and therefore have been excluded from recent global analyses of the conservation status of reptiles (Böhm et al. 2013, 2016; Meiri and Chapple 2016). So, it is unfortunate that 45 % of New Zealand lizard species are still undescribed.

The New Zealand Threat Classification System (NZTCS) that exists in New Zealand (Townsend et al. 2008) could inadvertently contribute to the situation. Unlike the IUCN Red List classification system, the NZTCS permits the inclusion of undescribed species. This has many advantages for lizards, as it allows putative newly discovered species to be assigned a conservation ranking (e.g. Hitchmough et al. 2016c) and resources to be rapidly directed towards its conservation management. But conversely, it may have the unintended consequence of alleviating the pressure to describe the species, as it is already formally recognised for conservation purposes within New Zealand. In adopting this approach, a proliferation of tag names is used (e.g. *Mokopirirakau* ‘Cupola’) to refer to species, some of which have been in use for more than 30 years without the formal description of the species (Hitchmough et al. 2016a), and a deviation from the Linnaean taxonomic system follows.

Another factor is that there have been no full-time lizard taxonomists in New Zealand since McCann’s (1955) revision of the native lizard fauna (Hitchmough et al. 2016a). Although 21 lizard species (18 skinks, 3 geckos) have been described since 1980, species descriptions have failed to keep up with the additional 66 extant species/taxa recognised over the same period (Hitchmough et al. 2016a). Lizard taxonomy in New Zealand has seemingly been relegated to something that interested researchers pursue in their spare time. For instance, over the past 30 years, Geoff Patterson has described 18 species (Patterson and Daugherty 1990, 1994; Patterson 1997; Chapple and Patterson 2007; Chapple et al. 2008a, b, 2011; Bell and Patterson 2008; Patterson and Bell 2009; Patterson et al. 2013), elevated two subspecies to species status (Patterson 1997), and reinstated the genus *Oligosoma* (Patterson and Daugherty 1995). What is even more remarkable about this achievement is that most of this has been accomplished whilst working full time at a bank!

A broader cross section of New Zealand herpetologists need to become involved in lizard taxonomic research in order to overcome the taxonomic impediment. After all, since the 1960s, it has taken an average of 16.5 years between the discovery of novel taxa until their formal description (data from Table 4.4, with undescribed species right-censored; Hitchmough et al. 2016a). Given that an average of 0.58 species has been described each year since 1980, if this rate continues, it will take a further ~80 years to describe the remaining 47 undescribed taxa that we are aware of (not to mention additional species that might be discovered during this time). However, there are promising signs these species descriptions may be published more quickly, as several major taxonomic works on geckos (R.A. Hitchmough, S.V. Neilsen, A. Bauer, unpublished data) and skinks (*O. infrapunctatum* and *O. lineoocellatum*-*O. chloronoton* species complexes: G.B. Patterson and S. Melzer, unpublished data; *O.* ‘Whirinaki’: B. Barr, D.G. Chapple, R.A. Hitchmough, unpublished data) are currently in advanced stages of preparation (Hitchmough et al. 2016a).

4. Limited Awareness of the Value of Natural History Collections Aside from Charles McCann, museum-based researchers have failed to play a major role in New Zealand lizard research (Chapple 2016). This has impacted the size and scope of the natural history collections for lizards, and the two major specimen collections in New Zealand (Te Papa Tongewara, Museum of New Zealand, Wellington; Auckland Museum, Auckland) are small relative to the diversity of the lizard fauna. Indeed, the situation could be worse if it was not for the fact that the Te Papa collection also incorporates the extensive specimen collection of the former Ecology Division (Department of Scientific and Industrial Research) and 1250 specimens from the collection of Charles Daugherty (Victoria University of Wellington). Despite this, these museum collections represent one of the most valuable resources available to New Zealand herpetologists, though they are surprisingly undervalued and underutilised.

The value of natural history collections extends beyond simply providing lizard species that can be used for species descriptions. They contribute to our knowledge of species distributions (and temporal changes in distribution), life history, reproduction, diet, and parasite ecology (e.g. Pettitt 1991; Kemp 2015). Yet, it is becoming increasingly difficult for researchers to collect tissue samples, or voucher specimens, of New Zealand lizard species. This may stem from the reluctance of the permitting agency (Department of Conservation) to permit specimen collection, or the failure of researchers to consult properly with iwi (Māori groups) about such research (it is often seen by researchers as a hurdle, rather than an opportunity to excite tangata whenua about the importance of their research and what they can do to help protect their taonga). This often applies even when researchers encounter unusual specimens or suspected new species, leading to attempts to subsequently identify these individuals based on photographs. Some of these taxa are unable to be found on subsequent field trips (e.g. *Oligosoma* 'Whirinaki' in Whirinaki Forest) and remain taxonomic enigmas today. Researchers are sometimes even denied permission to collect the voucher specimens that are required to formally describe new species (called type specimens). This represents another factor that has inhibited the rate of species description in New Zealand.

14.3 New Zealand Lizards: The Way Forward

As highlighted in this book, the New Zealand lizard fauna represents a fascinating study system. Because of its size, diversity, and ecological oddities, the New Zealand lizard fauna enables us to address a range of ecological, evolutionary, and physiological questions. Here I outline, in no particular order, the priority areas for future research on New Zealand lizards.

1. Comparative Osteological Studies of Extant New Zealand Lizard Species As highlighted by Worthy (2016), our interpretation of the lizard fossil record in New Zealand is constrained by limited comparative material from extant species, as well as by a lack of analyses of the intra- and interspecific variation in skeletal structures. It is therefore difficult to assign fossil material to extant species, which would provide an indication of the pre-human distribution of each lizard species, or whether it is from a distinct, now extinct species. This knowledge would not only improve our understanding of the biogeography and evolutionary history of New Zealand lizards but would also enable us to better quantify the post-human declines of the fauna. In a conservation context, it would allow potential mainland translocation or reintroduction sites to be identified. This field of study also represents one of the underappreciated potential uses of natural history collections in New Zealand (see Sect. 14.2).

2. Taxonomic Research and the Description of All Undescribed Lizard Species As highlighted throughout the book (Chapple 2016; Hitchmough et al. 2016a; Sect. 14.2), the large proportion (45 %) of undescribed lizard species in New Zealand has been an impediment to our understanding of the fauna. Conservation-focused researchers and government agencies need to better appreciate the urgent need for taxonomic work and the formal description of all remaining undescribed species. The completion of this work may require the specific allocation of funds (e.g. government grants) and other resources, along with greater support from permitting agencies to facilitate the collection of tissue samples and type species required for thorough and robust species descriptions.

3. Biogeographic Studies of New Zealand Lizards As emphasised by Chapple and Hitchmough (2016), the foundations have been laid for a golden age of New Zealand lizard biogeography. We now have a better grasp on the true diversity of lizard species in New Zealand (Hitchmough et al. 2016a) as well as of the current distribution of each species. If this was eventually combined with a better understanding of the pre-human distributions of each species, it would enable a broad range of biogeographic, and conservation biogeographic, studies to be completed. To date, most studies on the biogeography of New Zealand lizards have used a broad-brush, qualitative approach. Future studies now have an opportunity to adopt quantitative approaches to address fundamental biogeographic patterns and processes (e.g. Di Virgilio et al. 2014), or focus in on fine-scale or regional patterns (e.g. comparative studies on the impact of specific biogeographic barriers and studies of secondary contact among species or distinct genetic lineages). These investigations would increase our understanding of species-isolating mechanisms in New Zealand lizards, the process of reinforcement, and the drivers of speciation within this diverse fauna.

4. Detailed Studies on the Ecology, Reproduction, Life History, and Physiology of New Zealand Lizards Several chapters highlighted the large knowledge gaps that we have on the ecology (Hare et al. 2016), reproduction and life history (Cree and Hare 2016), and physiology (Hare and Cree 2016) of New Zealand lizard species. To rectify this situation, researchers should conduct well-designed, long-term field studies, specifically targeting poorly known species (see Sect. 14.2). Detailed studies are also required to address specific issues or questions, such as (1) vocalisations in geckos, (2) mating system and sociality (including investigation of hybridisation in both wild and captive populations), (3) how lizard species manage to persist in extreme alpine habitats (e.g. *O. pikitanga*, *O. judgei*, *Mokopirirakau kahutarae*), and (4) the potential impact of climate change on native lizard species. Some high-quality studies have already been conducted in this area (e.g. Penniket and Cree 2015), but further research is required on each topic.

5. Investigation of How Species Persist, Without Being Detected, in Mainland Locations with Mammalian Predators The recent discovery of a remnant Duvaucel's gecko (*Hoplodactylus duvaucelii*) individual within Maungatautari, a fenced mountain sanctuary in the Waikato region, North Island (Morgan-Richards et al. 2016; Nelson et al. 2016), indicates that some species have the ability to persist, undetected, in the presence of mammalian predators (e.g. Hoare et al. 2007). Research from an ecological and evolutionary perspective should be conducted into this issue, as it may generate knowledge that could facilitate the discovery of additional remnant populations on the main islands, as well as detect such 'stealth' populations on the offshore islands occupied by mammalian predators.

6. Quantitative Studies on the Value of Mainland Sanctuaries for Lizard Conservation Nelson et al. (2016) identified that there is a lack of quantitative data on the conservation benefit of mainland sanctuaries to lizards. Long-term field studies, using appropriate sampling and marking techniques (see Lettink and Hare 2016), are therefore required to compare lizard populations within, and outside of, the mainland reserves (and if possible, multiple sites of each should be used) and monitoring of predator populations. As outlined by Nelson et al. (2016), a rigorous, consistent trapping grid should be employed and a range of morphometric, behavioural, body condition, and physiological measurements taken to better quantify the potential sublethal impacts of mammalian predators. Although mainland sanctuaries have great potential for lizard conservation, such studies are essential in order to justify the conservation resources and efforts currently being devoted to them.

7. Quantify the Potential Impact of the Plague Skink on the New Zealand Biota Chapple et al. (2016b) highlighted that there have been no documented negative impacts of the plague skink. However, it is important to note that our ability to detect any impact has been limited as there has never been any dedicated research programme that aims to address this issue, either in New Zealand or elsewhere in its invasive range (Lord Howe Island, Hawaiian Islands; Chapple et al. 2013, 2014). Without this evidence, it becomes harder to justify to government and conservation managers why mitigation and/or eradication of the plague skink may be required. Current efforts to eradicate or mitigate the effects of plague skinks on Great Barrier Island represent an ideal opportunity to rectify this; it provides the perfect study system in which to investigate the lethal and sublethal (e.g. impacts on behaviour, life history, and/or body condition) effects of the plague skink on native skinks. This could be achieved by investigating and comparing native skink populations (or other faunal groups such as invertebrates) where they are sympatric, and allopatric, with plague skinks. Indeed, due to the wide distribution of the plague skink and the lower abundance of native lizard species, there are very few places in mainland locations on the North Island where there is this access to paired sites within the same region.

Acknowledgements I thank Kelly Hare and Mike Thompson for their thoughts about the current state, and future, of New Zealand lizard research.

References

Bartle JA (2016) Tony Whitaker: life and achievements of a pioneer New Zealand lizard ecologist. J R Soc N Z 46:3–15

Barwick RE (1959) The life history of the common New Zealand skink *Leiolopisma zelandica* (Gray, 1843). Trans R Soc N Z 86:331–380

Bell TP, Patterson GB (2008) A rare alpine skink *Oligosoma pikitanga* n. sp. (Reptilia: Scincidae) from Llawrenny Peaks, Fiordland, New Zealand. Zootaxa 1882:57–68

Böhm M et al (2013) The conservation status of the world's reptiles. Biol Conserv 157:372–385

Böhm M, Williams R, Bramhall HR, McMillian KM, Davidson AD, Garcia A, Bland LM, Bielby J, Collen B (2016) Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob Ecol Biogeogr 25:391–405

Chapple DG (2016) Synthesizing our current knowledge of New Zealand lizards. Chap. 1. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Chapple DG, Patterson GB (2007) A new skink species (*Oligosoma taumakae* sp. nov.; Reptilia: Scincidae) from the Open Bay Islands, New Zealand. N Z J Zool 34:347–357

Chapple DG, Patterson GB, Gleeson DM, Daugherty CH, Ritchie PA (2008a) Taxonomic revision of the marbled skink (*Cyclodina oliveri*, Reptilia: Scincidae) species complex, with a description of a new species. N Z J Zool 35:129–146

Chapple DG, Patterson GB, Bell T, Daugherty CH (2008b) Taxonomic revision of the New Zealand Copper Skink (*Cyclodina aenea*: Squamata: Scincidae) species complex, with descriptions of two new species. J Herpetol 42:437–452

Chapple DG, Bell T, Chapple SNJ, Miller KA, Daugherty CH, Patterson GB (2011) Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma inconspicuum*; Reptilia: Scincidae) species complex. Zootaxa 2782:1–33

Chapple DG, Miller KA, Kraus F, Thompson MB (2013) Divergent introduction histories among invasive populations of the delicate skink (*Lampropholis delicata*): has the importance of genetic admixture in the success of biological invasions been overemphasized? Divers Distrib 19:134–146

Chapple DG, Miller KA, Chaplin K, Barnett L, Thompson MB, Bray RD (2014) Biology of the invasive delicate skink (*Lampropholis delicata*) on Lord Howe Island. Aust J Zool 62:498–506

Chapple DG, Knegtmans J, Kikillus H, van Winkel D (2016a) Biosecurity of exotic reptiles and amphibians in New Zealand: building upon Tony Whitaker's legacy. J R Soc N Z 46:66–84

Chapple DG, Reardon JT, Peace JE (2016b) Origin, spread and biology of the invasive plague skink (*Lampropholis delicata*) in New Zealand. Chap. 13. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Di Virgilio G, Laffan SW, Ebach MC, Chapple DG (2014) Spatial variation in the climatic predictors of species composition turnover and endemism. Ecol Evol 4:3264–3278

Gardner MG, Pearson SK, Johnston GR, Schwarz MP (2016) Group living in squamate reptiles: a review of evidence for stable aggregations. Biol Rev. doi:10.1111/brv.12201

Gartrell B (2016) Diseases of New Zealand reptiles. Chap. 8. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hare KM, Cree A (2016) Thermal and metabolic physiology of New Zealand lizards. Chap. 9. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hare KM, Chapple DG, Towns DR, van Winkel D (2016) The ecology of New Zealand's lizards. Chap. 6. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Heath ACG, Whitaker AH (2015) Mites (Acari: Pterygosomatidae, Macronyssidae) taken from lizards intercepted at the New Zealand border. Syst Appl Acarol 20:739–756

Hitchmough RA, Patterson GB, Chapple DG (2016a) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chap. 4. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Hitchmough RA, Adams LK, Reardon JT, Monks JM (2016b) Current challenges and future directions in lizard conservation in New Zealand. J R Soc N Z 46:29–39

Hitchmough R, Barr B, Lettink M, Monks J, Reardon J, Tocher M, van Winkel D, Rolfe J (2016c) Conservation status of New Zealand reptiles, 2015. Department of Conservation, Wellington

Hoare JM, Pledger S, Nelson NJ, Daugherty CH (2007) Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. Biol Conserv 136:510–519

IUCN (2016) The IUCN red list of threatened species. http://www.iucnredlist.org/. Accessed 2 May 2016

Kemp C (2015) Museums: the endangered dead. Nature 518:292–294

Lettink M, Hare KM (2016) Sampling techniques for New Zealand lizards. Chap. 10. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Lettink M, Monks JM (2016) Survey and monitoring methods for New Zealand lizards. J R Soc N Z 46:16–28

McCann C (1955) The lizards of New Zealand. Gekkonidae and Scincidae. Dominion Museum Bulletin, 17

Meiri S, Chapple DG (2016) Biases in the current knowledge of threat status in lizards, and bridging the ‘assessment gap’. Biol Conserv. doi:10.1016/j.biocon.2016.03.009

Morgan-Richards M, Rheyda Hinlo M, Smuts-Kennedy C, Innes J, Ji W, Barry M, Brunton D, Hitchmough RA (2016) Identification of a rare gecko from North Island New Zealand, and genetic assessment of its probable origin: a novel mainland conservation priority? J Herpetol 50:77–86

Nelson NJ, Hitchmough R, Monks JM (2014) New Zealand reptiles and their conservation. In: Stow A, Maclean N, Holwell GI (eds) Austral Ark: the state of wildlife in Australia and New Zealand. Cambridge University Press, Cambridge, pp 382–404

Nelson NJ, Romijn RL, Dumont T, Reardon JT, Monks JM, Hitchmough RA, Empson R, Briskie JV (2016) Lizard conservation in mainland sanctuaries. Chap. 12. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Patterson GB (1997) South Island skinks of the genus *Oligosoma*: description of *O. longipes* n. sp. with redescription of *O. otagense* (McCann) and *O. waimatense* (McCann). J R Soc N Z 27:439–450

Patterson G, Bell T (2009) The Barrier skink *Oligosoma judgei* n.sp. (Reptilia: Scincidae) from the Darran and Takitimu Mountains, South Island, New Zealand. Zootaxa 2271:43–56

Patterson GB, Daugherty CH (1990) Four new species and one new subspecies of skinks, genus *Leiolopisma* (Reptilia: Lacertilia: Scincidae) from New Zealand. J R Soc N Z 20:65–84

Patterson GB, Daugherty CH (1994) *Leiolopisma stenotis* n. sp., (Reptilia: Lacertilia: Scincidae) from Stewart Island, New Zealand. J R Soc N Z 24:125–132

Patterson GB, Daugherty CH (1995) Reinstatement of the genus *Oligosoma* (Reptilia: Lacertilia: Scincidae). J R Soc N Z 25:327–331

Patterson GB, Hitchmough RA, Chapple DG (2013) Taxonomic revision of the ornate skink (*Oligosoma ornatum*; Reptilia: Scincidae) species complex from northern New Zealand. Zootaxa 3736:54–68

Penniket S, Cree A (2015) Adherence to Bergmann’s rule by lizards may depend on thermoregulatory mode: support from a nocturnal gecko. Oecologia 178:427–440

Pettitt C (1991) What price natural history collections, or ‘Why do we need all these bloody mice?’. Mus J 91:25–28

Shea GM (2016) History of discovery of the New Zealand lizard fauna. Chap. 2. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Tingley R, Hitchmough RA, Chapple DG (2013) Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol Conserv 165:62–68

Towns DR (1975) Ecology of the black shore skink, *Leiolopisma suteri* (Lacertilia: Scincidae), in boulder beach habitats. N Z J Zool 2:389–407

Towns DR, Hitchmough RA, Perrott J (2016a) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? Chap. 11. In: Chapple DG (ed) New Zealand lizards. Springer, Cham

Towns DR, Miller KA, Nelson NJ, Chapple DG (2016b) Can translocations to islands reduce extinction risk for reptiles? Case studies from New Zealand. Biol Conserv. doi:10.1016/j.biocon.2016.04.024

Townsend AJ, de Lange PJ, Duffy CAJ, Miskelly CM, Molloy J, Norton D (2008) New Zealand threat classification system manual. Department of Conservation, Wellington

Whitaker AH (1968) The lizards of the Poor Knights Islands, New Zealand. N Z J Sci 11:623–651

Whitaker AH (1973) Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). Proc N Z Ecol Soc 20:121–130

Worthy TH (2016) A review of the fossil record of New Zealand lizards. Chap. 3. In: Chapple DG (ed) New Zealand lizards. Springer, Cham