

Alien Reptiles and Amphibians

a Scientific Compendium and Analysis

Fred Kraus



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Alien Reptiles and Amphibians

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Fred Kraus

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A Scientific Compendium and Analysis



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*For Ezra, in gratitude for her gracious love
and tolerance*

Preface

Transportation of species to areas outside their native ranges has been a feature of human culture for millennia. During this time such activities have largely been viewed as beneficial or inconsequential. However, it has become increasingly clear that human-caused introductions of alien biota are an ecological disruption whose consequences rival those of better-known insults like chemical pollution, habitat loss, and climate change. Indeed, the irreversible nature of most alien-species introductions makes them less prone to correction than many other ecological problems. Current reshuffling of species ranges is so great that the present era has been referred to by some as the “Homogocene” in an effort to reflect the unique magnitude of the changes being made.

These alien interlopers often cause considerable ecological and economic damage where introduced. Species extinctions, food-web disruptions, community alterations, ecosystem conversion, changes in nutrient cycling, fisheries collapse, watershed degradation, agricultural loss, building damage, and disease epidemics are among the destructive – and frequently unpredictable – ecological and economic effects that invasive alien species can inflict. The magnitude of these damages continues to grow, with virtually all environments heavily used by humans now dominated by alien species and many “natural” areas becoming increasingly prone to alien invasion as well.

Attention to this problem has increased in the past decade or so, and efforts to prevent or limit further harm are gaining wider scientific and political acceptance. Scientific and managerial attention to invasive aliens is not, however, distributed equally across all plant and wildlife species. Most research and management efforts involving terrestrial invasives have been showered on mammals, plants, and insects. This is unsurprising because many of these organisms cause tremendous amounts of damage, so focus on them is reasonable and justified. But this practice also leads to an often unstated presumption that those alien organisms not featured in books, newspapers, magazines, or scientific journals must not be causing problems. That may be true; but it need not be, and it may not be as a general rule. The rub, of course, is that the only way to be sure of presumptive harmlessness is to directly investigate the less-recognized, unstudied alien species – studies lacking precisely because of the presumption. Thus are we mired in a Catch-22.

Reptiles and amphibians are among those alien taxa whose introductions have largely been ignored. And yet their introduction has become common and widespread, although it is difficult to appreciate the scale of this phenomenon from the widely scattered references in a frequently obscure literature. Partly for this reason, herpetological introductions have received scant attention from policy makers, land managers, and researchers. Hence, a scientific compendium of the topic is warranted, and I attempt to provide that here. I present here a database of amphibian and reptile introductions – based on the published literature and of global ambit – so as to analyze how these introductions are occurring. The database is provided in Appendix 1 and comprises a large portion of the present book. Complementary to this is a bibliography of approximately 4,000 supporting references.

But what matters as much as providing these raw data is placing them in context and determining what they signify. This is addressed in the several chapters that precede the database. Because this book is not addressed solely to specialists on invasive species, the first chapter provides a short overview of alien invasions and human responses, then briefly summarizes the history of how study of herpetological invasions has developed. The remaining chapters focus on alien reptiles and amphibians in particular. Chapter 2 uses the database to analyze how reptiles and amphibians have been transported by humans and how those patterns change spatially and through time. Knowledge of these mechanisms and patterns is requisite for preventing future introductions. Chapter 3 summarizes the detrimental impacts documented to result from introductions of alien herpetofauna. Chapter 4 examines management responses that have been taken against herpetological invasions and what factors limit the effectiveness of those responses. The final chapter examines the logical implications that the data presented in earlier chapters have for designing appropriate management programs. It also identifies research needs for improving understanding and management of reptile and amphibian introductions. Comprehensive summaries or analyses of the topics treated in Chapters 2–5 are currently lacking in the literature.

I take it as axiomatic that scientists have a responsibility to help society solve its problems and challenges. Consistent with this belief, this book is explicitly concerned with applying scientific data to a practical conservation problem; hence, the book may appear more applied than is common for the standard academic tome. I have three aims for this book. The first is to document that alien reptiles and amphibians are a valid conservation problem that warrants a broader management response than it has yet received. Chapters 2 and 3 are most relevant to that goal. Evidence contained in both should improve recognition within the scientific and policy-making communities of the magnitude of herpetofaunal changes now occurring and, ideally, stimulate more action toward ameliorating this unprecedented and uncontrolled experiment in biological mixing. The current evidence suggests that continued managerial inaction is not a responsible option.

The second goal is to identify what managerial and research actions are necessary to meet this conservation challenge. Accordingly, I examine what practical and research efforts have been directed toward these organisms and suggest how both pursuits can be improved. So as to make it logistically easier for future research to

proceed I provide the database compiling the majority of the published literature on this topic. There is increasing interest in invasive reptiles and amphibians among students, but it is commonly difficult for them to discover relevant literature. In providing a compilation of introductions and the large majority of their supporting literature in one source I hope to make it more attractive and feasible for a new generation to pursue research on the ecological and evolutionary ramifications of these introductions, as well as their solutions.

Thirdly, much of the aesthetic and ecological harm inflicted on native herpetofaunas by alien introductions stems, ironically, from the activities of many who have a love for these animals. This book will make clear the extent to which careless or arrogant pet fanciers and an indifferent pet industry have been responsible for this harm. It is my hope that making this pattern clear will lead to some critical self-examination and behavioral changes among this cohort of herpetophiles.

A special circle in heaven is reserved for those who have assisted me with obtaining literature incorporated into this database or used in the introductory chapters. I am happy to report that Harald Artner, Aaron Bauer, Mark Bayless, Mary Bomford, Lea' Bonewell, Roger Bour, Chris Buddenhagen, Russ Burke, Earl Campbell, Todd Campbell, Jack Crayon, Ron Crombie, Indraneil Das, Chris Dionigi, Sandy Echnacht, Kevin Enge, Antoine Fouquet, Tom Fritts, Darrel Frost, Pam Fuller, Trent Garner, Eli Greenbaum, Heinz Grillitsch, Ivan Ineich, John Iverson, Fabio Jaksic, Mark Jennings, Erik Johnson, Haruki Karube, David Kizirian, Ken Krysko, Kriton Kunz, Skip Lazell, Tim Low, Ann Marsteller, Roy McDiarmid, John Measey, Jesus Mellado, Paul Moler, Ron Nussbaum, Kimiko Okabe, Isamu Okochi, Hidetoshi Ota, Gad Perry, Robert Powell, Edoardo Razzetti, Robert Reed, Constance Rinaldo, Gordon Rodda, Martha Rosen, Phil Rosen, Pete Savarie, Riccardo Scalera, Patrick Schembri, Greg Schneider, Brad Shaffer, Glenn Shea, Dawn Skala, John Slapcinsky, Pritpal Soorae, Gill Sparrow, Thomas Ulber, Mark Wilkinson, Lori Williams, Julie Wycherley, and George Zug will all be residing in ethereal splendor upon relinquishing this mortal realm. In this vein, the choicest perquisites will be reserved for Aaron Bauer, Ron Crombie, Darrel Frost, David Kizirian, Roy McDiarmid, Hidetoshi Ota, Greg Schneider, Jens Vindum, and George Zug for facilitating my repeated access to their personal or institutional libraries or for sending me many relevant articles. Of considerable help in amassing literature were Pomai Estrella and Ellen Pyle, who worked long on my behalf to track down difficult-to-obtain literature sources. I also thank the library staffs at Bishop Museum and University of Hawaii for obtaining many articles for me. I am greatly indebted to Philip Thomas (Hawaiian Ecosystems at Risk Project) for providing much advice and assistance maintaining and querying this database; Ron Crombie for critically reviewing an earlier version of the database for completeness and nomenclatural currency; Chris Buddenhagen, Lloyd Loope, Gad Perry, and Gordon Rodda for helpful discussions and reviewing drafts of some of the chapters; and Thurid Campbell, Fern Duvall, Jaap Eizenga, Fan Gao, Denis Kasatkin, George Phocas, and Naomi Sugimura for providing translations of original articles. I thank the individuals whose personal communications are cited throughout the book for the helpful information and discussions they provided me. I especially thank Earl Campbell for his unstinting support of this project.

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Lastly, I thank Jim Carlton and Greg Ruiz for inviting me to contribute an analysis of reptile and amphibian introductions to a workshop organized by the Global Invasive Species Program in 1999. Without this initial impetus I never would have embarked on such a fool's errand.

Fred Kraus

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Chapter 1

Background to Invasive Reptiles and Amphibians

Concern about invasive alien species is a relatively new phenomenon that can be dated to the work of Charles Elton, the ecologist who provided the first thorough scrutiny of the topic. Elton (1958) demonstrated the severe ecological and human-health impacts that invasive alien species can cause. Since then, the number of introduced species has skyrocketed, and examples are now available to illustrate a much larger array of resulting damages. The spatial scale of ecological harm resulting from alien invasions also continues to grow because virtually all environments heavily impacted by humans are now dominated by alien species. Many “natural” areas are also increasingly subject to alien invasion.

Scientific interest began to gather momentum in the 1980s, spurred by the publication of several edited books on this topic (Groves and Burdon, 1986; Mooney and Drake, 1986; Drake et al., 1989). Many scientific (e.g., M. Williamson, 1996; Mooney and Hobbs, 2000; Perrings et al., 2000; McNeely, 2001; Mooney et al., 2005; Nentwig, 2007) and popular (e.g., Bright, 1998; Devine, 1998; G.W. Cox, 1999; Low, 1999; Van Driesche and Van Driesche, 2000; Baskin, 2002) books on the issue have appeared as concern with the impacts of alien species became more widespread. A journal specifically devoted to the topic of biological invasions was founded in 1999, and the field is increasingly replete with scientific studies addressing the dynamics and ecological processes of invasion. There is also a recent spate of books treating either specific aspects of the invasive-species problem or summarizing the status of the topic in particular geographic regions. In short, the topic is now well established in the scientific mainstream, is attracting concerned attention among a wider public, and is increasingly recognized as one of the premier environmental challenges of the new century.

In order to provide context and background information for considering the phenomenon of invasiveness in reptiles and amphibians, this chapter presents a brief introduction to invasive-species biology.

What Is an Invasive Species?

Terminology regarding invasive species has proliferated and changed through the years, and a potentially confusing array of descriptors is available (Davis and Thompson, 2000; Richardson et al., 2000a; Daehler, 2001). I use the term “alien

species” to refer to those species transported and released outside their native ranges by the activities of humans, whether done intentionally or not. The movement of such a species by humans is referred to as an “introduction”. Not all introduced species become established, but many do. Such established populations are often referred to as “alien”, “naturalized”, “non-native”, “non-indigenous”, “feral”, or “exotic”, but I will confine myself to the first two terms.

Human-mediated dispersal of species is not necessarily a *qualitatively* different phenomenon than dispersal by other means, such as attaching to a bear’s fur or a waterbird’s foot. However, the temporal and spatial scales at which humans are homogenizing the world’s biota are of a far greater magnitude than previously seen in Earth’s history. As one example, Loope (1998) estimated that prior to human arrival, the rate of new species establishment in the Hawaiian Islands was approximately 1 species/35,000 years. Now it is on the order of 20–30 species/year (Beardsley, 1962, 1979; Miller and Holt, 1992), an approximately million-fold rate increase. Similar changes have occurred on other oceanic islands and in marine and freshwater systems (Ricciardi, 2007), although with perhaps not so extreme a rate increase as in Hawaii. Establishment rates on continents seem to be lower but are already far above historical rates and appear to be increasing. From a spatial perspective, species are now being mixed among continents that have not been connected for 250 million years. As well, species having limited mobility – such that they would not previously travel even to locations a short distance away – are now spread around the world by human activity. This overwhelming increase in rate and areal extent of alien-species introductions has had profound effects on native species and ecosystems throughout the globe. Hence, restricting use of the term “alien” to those species introduced by humans provides a very practical distinction for scientific and management purposes.

Invasive species are that subset of alien species having a demonstrated negative effect on native ecosystems, species, or human values and concerns. Invasive species are often referred to as either “weeds” or “pests” as well, and if impacts are largely incurred by natural ecosystems the species may be termed an “environmental pest”. The distinction between alien and invasive species may be made clearer by a few examples. Corn (*Zea mays*) is an alien species everywhere on Earth outside of southern Mexico, but it is invasive nowhere because it fails to establish outside the artificial ecological conditions imposed by agriculture. Many alien species – including most important crop species – are like this, growing only where deliberately planted, or living in sparse numbers in the wild, to all appearances having no deleterious effects on native or human ecosystems. But invasive aliens – such as brown treesnakes, gypsy moths, cheatgrass, or bubonic plague – are another matter entirely. They spread throughout areas to which they are introduced and cause tremendous harm to wildlife, agriculture, or human health. Escaping one or more forms of ecological constraint allows them to achieve unregulated population growth, forming the ecological equivalent to cancerous cell proliferation within an organism. The process by which an alien species establishes, expands its geographic range and numbers, and exerts ecological or economic impacts in a new locality is referred to as “invasion”.

Invasive species are usually thought to comprise a relatively modest subset of all alien species (Williamson and Fitter, 1996), but this conclusion bears two important caveats. First, this view may partly reflect our limited anthropocentric perspective, and it is certainly a function of the degree to which we have attempted to identify invasives. When investigated from the standpoint of impacts on other species, such as native insects, it may turn out that far more alien species have negative ecological effects than we currently appreciate and should be viewed as invasive pests. Hence, our impression of the percentage of alien species formed by invasive pests may rise with passing time and increased research effort, as suggested by recent findings indicating higher rates of establishment (Kraus, 2003c) and spread (Jeschke and Strayer, 2005) among animals than earlier predicted (Williamson and Fitter, 1996). Second, although most pests prove invasive in many or most areas where introduced, some species prove invasive or pestiferous in only one or a few localities but appear harmless in most areas where introduced. There are a number of examples of this phenomenon, such as the traveller's palm, *Ravenala madagascariensis*, that is widely and benignly planted throughout the tropics but has become an invasive pest in the Mascarene Islands (Cronk and Fuller, 1995). Consequently, one must be careful in extrapolating from an observation of non-invasiveness in one locality to infer safety in other areas. Because of our imperfect knowledge of the ecological consequences of mixing biotas, caution is required in asserting that any alien species poses no hazard. Prudence and expanding scientific understanding both dictate that the burden of proof lies on those who would argue that an introduction is harmless. This has practical consequences for designing effective management responses for invasive species, a point that will be discussed at greater length in the final chapter.

Two Misconceptions

One sometimes hears claims that the introduction of alien species is a normal, if not always positive, phenomenon that does not merit concern. One such argument is that introducing alien species serves to increase biological diversity (or "biodiversity") within a region. Because establishment of an alien species increases the total number of species – naively thought to equate to biodiversity – alien species are good, the argument goes. This argument is fallacious for two reasons. First, biodiversity is not measured as just the summary number of species in an area but also includes some measure of the relative abundances of the assembled species. Diversity is not enhanced when one species dominates over everyone else. If many (native) species are present but rare and one (invasive) is supremely common, biodiversity is relatively low, even if the number of species is one greater than it was prior to the invasion. This is exactly how invasive species tend to behave, so they frequently decrease biodiversity. Secondly, the scale at which biodiversity is measured is crucial. In particular, one must carefully distinguish among diversity measures at different geographical scales. Obviously, increasingly larger regions

contain greater biodiversity than do any of their smaller, constituent subregions. My backyard in Honolulu is not very diverse; Honolulu is somewhat more diverse; the island of Oahu is yet more diverse; the entire chain of Hawaiian Islands is still more diverse; the Pacific Basin is yet more diverse; and the entire world is the most diverse. Different processes are involved in generating diversity at different geographic scales (Sax and Gaines, 2003), and this can potentially confuse discussion of biodiversity. In speaking of recent concerns for biodiversity protection, we are speaking of preserving diversity at the largest scale – that is, ensuring that the sum total of diversity on the entire planet is not diminished. Conceptually, this is a simple matter of ensuring that species extinction does not occur. Hawaii has many species unique to that archipelago. If we artificially inflate species numbers by importing alien species that cause the extinction of Hawaii's unique species, we may have boosted species numbers within Hawaii but at the cost of the global total. Replacement of globally unique elements by artificial inflation of regional species numbers with widespread aliens is not a service to biodiversity, but rather the converse: it decreases biological diversity. And indeed, introduced species are among the major drivers of biotic homogenization, the process by which formerly distinct biotas are beginning to look more and more alike (McKinney and Lockwood, 1999).

One also frequently hears the argument that species movements are “natural” and that concern about alien species is, therefore, unjustified. This claim too is specious. For the term “natural” to apply in any scientifically meaningful way it must refer to a phenomenon occurring at background ecological temporal (the rate at which a phenomenon occurs) and spatial (geographic) scales. As I have mentioned earlier, introduction rates in Hawaii are now approximately one million times as frequent as the natural, background rate. Similar high rate increases have been measured for other regions too (Ricciardi, 2007). The geographical reach of species transport by humans also extends far beyond what the organisms could have achieved under natural processes. To give just one example, there is no way that chameleons – ponderous arboreal lizards native to Africa and western Asia – could possibly have colonized places as remote as Hawaii or California under their own power. The geographical barriers that helped give rise to the tremendous and regionally unique biological diversity across Earth are proving ineffectual in the face of human modes of transport such as ships and planes. Moreover, the number of species and individuals moved during each introduction event is often now much larger than could have occurred under natural conditions (Ricciardi, 2007). For example, a single load of ballast water may dump millions of individuals of hundreds of species, a form of dispersal unparalleled in pre-human history. In short, there is nothing remotely natural about the tempo and extent of modern biological mixing by human action.

Another variant of this argument is to posit that because humans are a part of the natural world, anything we do is also natural and, hence, no cause for worry. Under this reasoning, our transport of alien species is natural and we shouldn't be overly concerned with it. Of course, by that same logic, genocide, torture, and slavery are natural too. I doubt that most readers would find these other human actions

compellingly justified by so cavalier an argument. So it is with alien species. There is nothing remotely natural about the Homogocene, and arguments that pretend that this is the case are contrary to the evidence. Consequently, this book is written from the viewpoint that alien invasions – including those by reptiles and amphibians – are a serious ecological threat that demands attention and remediation.

The Invasion Process

In the past 20 years or so considerable scientific attention has been directed to understanding invasive species biology and how a species becomes invasive. Conceptually, the invasion process involves three stages: transport and release of the organism to a novel geographic area, establishment of a population in the new area, and expansion of the original population to fill ecological space beyond its point of entry. The biological and social factors that favor success in any one of these steps may not be the same as those favoring success in others (cf. Duncan et al., 2003). For example, successful transport may rely on the ability of a species to survive food deprivation for long periods or to tolerate harsh environmental conditions. Some perceived human benefit from the species, of course, also weighs heavily in the choice of those species that are deliberately introduced. Once arrived in the new habitat, population establishment requires that the climate be survivable, that appropriate food be available, and that reproduction be possible. Once established, rapid expansion may rely on access to food sources underutilized by native species, ability to avoid resident predators, or absence of debilitating disease organisms. As a consequence of these varied requirements, many organisms may fail to survive transport, those that do may fail to establish populations, and many that initially establish populations may fail to persist or to expand their ranges. To understand invasions, then, requires knowledge of how all three stages in the process are successfully negotiated by the invading species.

Transport

A host of pathways serves to introduce alien species to new environments. Unintentional introductions largely result from species hitch-hiking rides in cargo or on the vehicles used in transport. Examples include brown treesnakes (*Boiga irregularis*) being transported in wheel wells of aircraft, geckos stowing away in a variety of cargo shipments or the containers used to package cargo, plankton moved in the ballast water of ships, sessile marine invertebrates riding on the hulls of ships, and insects infesting grain shipments. Also included in this category are disease-causing agents moving about on infected humans (e.g., AIDS, malaria), their domesticated animals (e.g., rinderpest, avian influenza), or other vectors (e.g., dengue in mosquitoes travelling in used tires, cholera travelling in ballast water).

Intentional introductions occur primarily because a species is perceived to provide an amenity or use value to humans. Under this category fall introductions for use as pet animals, furs, human or livestock food, horticulture, and biocontrol of pests. Included as well are introductions and releases undertaken by individuals simply because they like a particular species and wish to be able to see it in their surroundings. As a rule, some taxonomic groups, such as marine invertebrates, insects, and landsnails are largely dispersed via unintentional pathways. Others, primarily plants, fish, birds, and mammals have largely been intentionally dispersed by humans. As I will demonstrate later, reptiles and amphibians are somewhat unusual in that they are transported via a diversity of intentional and unintentional pathways.

In considering intentional introductions, human selectivity ensures that those species introduced do not represent a random selection of all available species. Instead, species chosen for introduction can be biased taxonomically, geographically, and in having particular characteristics such as large body size, tasty flesh, or large population sizes (Blackburn and Duncan, 2001a; Duncan et al., 2003). In addition, they are often especially hardy, an attribute of obvious importance if a species is to be used for a purpose. Although this is intuitively obvious, the phenomenon has been quantified for few taxa. Recipient areas can also vary in being primarily islands (Blackburn and Duncan, 2001a; Kraus, 2003c) or continents (Kraus, 2003c), depending on the taxon in question.

Establishment

The naturalization process – the means by which a species establishes a reproducing population once transported to a new region – is not yet understood in great detail. Ideally, we would like to be able to learn enough to predict with reasonable certainty how likely a particular alien species is to naturalize in a particular area should it be introduced. But the particularities of both species and location that may be involved in any given introduction make generalization across all introductions difficult. This is because establishment success results from the interaction of the singular combination of biotic and abiotic needs of a species with the particular set of environmental conditions at the receiving location. Ideally, ability to predict naturalization success would allow us to prohibit importation of species deemed at high risk of establishment. Although we have not yet reached that point, several important generalities are becoming apparent.

First, it is important that the newly attained region provide a favorable environment. Logically, the climate must be sufficiently similar to that in the native range that a species' physiological tolerance is not exceeded. Consequently, climate matching has repeatedly been found to be an important predictor of establishment success (Blackburn and Duncan, 2001b; Duncan et al., 2001, 2003; Bomford and Glover, 2004; Forsyth et al., 2004; Hayes and Barry, 2008). The importance of climate is sufficiently uncontroversial that modeling an alien species' anticipated

potential range based on matching climatic variables from its native range is increasingly common (e.g., Peterson and Vieglais, 2001; Thuiller et al., 2005; Ficetola et al., 2007a). Second, the alien must have sufficient resources available to complete its life cycle. At a minimum, this means sufficient food, living space, habitat for growth and reproduction, and whatever other biotic factors, such as pollinators, may be required. This is thought to be made easier if the intruder possesses adaptive features lacking in the biota of its newly inhabited range, thus allowing it to pursue its way of life unhindered by close competition. Third, favorability of the introduced range may also be increased by the absence of predators, parasites, and disease organisms from the alien's native range. Leaving these enemies behind often gives an alien species a considerable competitive advantage over the natives it meets in its new home.

It is also clear that propagule pressure – the number of individuals released into a new area – is an important determinant of successful establishment. Those species that have been released more often, at more sites, or in greater numbers tend to establish more successfully than those that do not (M. Williamson, 1996, 1999; Duncan et al., 2001, 2003; Forsyth and Duncan, 2001; Kolar and Lodge, 2001; Bomford and Glover, 2004; Forsyth et al., 2004; Lockwood et al., 2005; Rejmánek et al., 2005; Caley and Kuhnert, 2006; Jeschke and Strayer, 2006; Hayes and Barry, 2008), although it can take many introductions to make this pattern statistically apparent (e.g., Ruesink, 2005; Bomford et al., in press). The larger the number of individuals released at a given site, the lower the chance of stochastic extinction (extinction due to bad luck randomly happening to strike all released individuals). Similarly, releases at more sites increase the odds that at least one population will survive by effectively sampling the environment for habitat most suitable to the introduced alien. Finally, a larger number of independent releases will likely sample a greater representation of genetic diversity from within the introduced species, providing greater genetic and (potentially) phenotypic variation with which to meet the ecological and evolutionary challenges of the new environment (Lockwood et al., 2005).

Unsurprisingly, life-history and behavioral characteristics of the introduced species can be important in determining establishing success (Reichard and Hamilton, 1997; Sol and Lefebvre, 2000; Duncan et al., 2001; Kolar and Lodge, 2001, 2002; Cassey, 2002; Cassey et al., 2004; Forsyth et al., 2004; Rejmánek et al., 2005; Ruesink, 2005; Jeschke and Strayer, 2006; Thuiller et al., 2006; Hayes and Barry, 2008). Such attributes vary among taxa and may even vary within the same taxon, either because different genotypic samples are involved or because different environments may induce different phenotypic effects. This idiosyncrasy again limits the taxonomic scope across which we may identify biological traits predictive of establishment success. This makes attaining useful generalizations for a broad array of taxa a laborious undertaking.

One of the most useful predictors of establishment success is whether a species has already successfully established somewhere else (Reichard and Hamilton, 1997; M. Williamson, 1999; Duncan et al., 2001; Forsyth et al., 2004; Caley and Kuhnert, 2006; Hayes and Barry, 2008). This is obviously not a very refined tool for predictive use. It doesn't carefully discriminate among introductions to different

habitats, and it is useless for all those species not yet transported by humans. One consequence of our limited predictive abilities is that practical governmental efforts to assess risk from alien species may focus on the hazards a species poses, rather than the likelihood of its establishment or spread (e.g., Bomford, 2003).

Interestingly, the extent to which the recipient location has already been invaded by other species can impinge on establishment success of new arrivals. Earlier invasions may synergistically facilitate the success of later invasions – and thereby magnify impacts on native ecosystems – in a process referred to as “invasional meltdown” (Simberloff and Von Holle, 1999). This occurs when earlier invaders provide resources – in the form of food, nutrients, pollination services, mycorrhizal associations, seed dispersal, or habitat – critical to the successful survival of later-arriving aliens. For example, the blind snake, *Ramphotyphlops braminus*, could not have survived introduction to Hawaii without its alien food sources (ants, termites) being introduced first. In this instance, the snake is ecologically benign, but many facilitated introductions are not. Facilitation frequently takes the form of acquisition of novel mutualisms among species (Simberloff and Von Holle, 1999; Richardson et al., 2000b), but it may also be effected by alterations of habitats, resource-supply rates, or disturbance regimes (Simberloff and Von Holle, 1999; Richardson et al., 2000b; Ricciardi, 2005) or by protection from predators or competitors (O’Dowd et al., 2003; Grosholz, 2005). These mutualisms may re-unite species that co-evolved together and were independently transported to the new location, but more often they involve generalists that can successfully form mutualistic pairings with a wide array of potential partners (Richardson et al., 2000b). Moreover, an alien may successfully establish but not become invasive until a facilitator species is later introduced (cf. Grosholz, 2005). The importance of invasional meltdown is that it provides a positive-feedback loop that makes recipient habitats more prone to additional invasions, accelerates the accumulation rate of alien species, and magnifies impacts. This phenomenon makes invasion and ecological disturbance more likely to occur over time, raising the concern that the rate of establishment, as well as the magnitude of impacts, may be increasing. It also makes predicting the impacts of any particular introduction more difficult.

We may also assess establishment success from a broader, community-level perspective. In this case, alien species richness (number of naturalized alien species) has been correlated with a variety of factors in an attempt to identify whether particular areas or habitat types are more prone to alien invasion. Regional richness in alien species has been correlated with human population numbers, land area, disturbance, and native-species richness, and these may vary in importance across spatial scales (Lonsdale, 1999; McKinney, 2001; Sax, 2002). With respect to human population, temporal growth in numbers of naturalized aliens has been correlated with increasing human population (Mauchamp, 1997; K.G. Smith, 2006a), and spatial variation in species richness has been correlated with variation in human population numbers (McKinney, 2001, 2002; Espinosa-Garcia et al., 2004; Gido et al., 2004). Many of these correlations are not ecologically surprising. Increasing land area should generally lead to increased species numbers because larger areas tend to hold greater habitat diversity, which will itself be correlated with increased

numbers of native species. Disturbance is well known to facilitate establishment and spread of many alien species, and it too is correlated with human numbers. While these correlations can often allow us to roughly predict which areas are likely to host increased alien species richness, they are silent with respect to establishment mechanisms and, hence, are not predictive in a manner that can readily be used to prevent individual future naturalizations.

Spread

Naturalized populations can vary tremendously in their ecological dominance, ranging along a continuum from those that barely hang on in small numbers at a single locality to those that spread like wildfire over a large range and become numerically dominant. Obviously, those at the latter end of the spectrum are clearly invasive, those at the former end are not, and opinions would differ about where along the continuum one might divide “invasive” from “non-invasive”. We would like to have an understanding of why these differences occur, as that would allow us to predict both the likelihood that any particular species would prove invasive as well as the relative susceptibility of particular locations to invasion.

A variety of hypotheses has been advanced to explain invasion success (reviewed in Hufbauer and Torchin, 2007). Ecological hypotheses include the notions that invaders are preadapted to the new environment, are inherently superior competitors, have novel adaptive mechanisms giving them a competitive edge over natives, have escaped from enemies that limit their population sizes in their native ranges, or interact with other introduced organisms in a positive-feedback loop that promotes population expansion. As well, ecological attributes of the invaded environment may serve to promote or to limit introduced species. In particular, the empty-niche hypothesis suggests that invasive species may use resources ignored or underutilized by natives. Conversely, the biotic-resistance hypothesis posits that natives that are close relatives of introduced species may serve to limit the expansion of the latter via competition or increased likelihood of parasite transferral. As well, invasion may be promoted by genetic changes within the introduced species. Hybridization, either with closely related natives or among populations of the introduced species from disparate parts of its native range, may increase genetic variation and allow for rapid creation of novel genotypes that are better suited to exploiting the new environment. Founder events may create new genotypes with similar ecological effect. Alternatively, the novel environment may impose a novel selective regime that promotes improved competitive ability among the invaders. In particular, release from enemies may allow energy resources that would otherwise be expended on defense to be used instead to promote growth and reproduction. Empirical support for each of these hypotheses is available for one invasion or another, although examinations of the genetic and evolutionary consequences of introductions have barely begun. Compellingly testing the empty-niche and biotic-resistance hypotheses has proven difficult because of the complexity of biotic interactions involved in

assessing predictions based on community-level parameters. Unsurprisingly, mechanism importance will vary with the biological particularities of each invading species, so generalizations have been difficult to clearly identify. It is important to recognize too that some of these hypotheses are not mutually exclusive, and the proposed mechanisms may interact with each other synergistically (Blumenthal, 2005; C.E. Mitchell et al., 2006). Attempts to integrate several of these specific hypotheses into more general theoretical frameworks have recently been made (Shea and Chesson, 2002; Facon et al., 2006). These synthetic perspectives provide a variety of specific predictions (C.E. Mitchell et al., 2006; Hufbauer and Torchin, 2007) whose future testing may better explain the diversity of outcomes of species introductions, potentially making identification of high-risk invaders more successful.

The difficulty of testing these ecological and genetic hypotheses has resulted in more attention being directed toward identifying characteristics of the introduced species themselves that might prove predictive of invasiveness. Unsurprisingly, many of the same features important in favoring establishment of species also tend to explain invasiveness, in particular, degree of climate-matching between native and introduced ranges (Duncan et al., 2001; Forsyth et al., 2004; Thuiller et al., 2005), and an assortment of life-history or other biological variables (Pheloung et al., 1999; Duncan et al., 2001; Kolar and Lodge, 2001, 2002; Williams et al., 2002; Daehler et al., 2004; Forsyth et al., 2004; Rejmánek et al., 2005; Pyšek and Richardson, 2007). As with predicting establishment, however, it is clear that generalities will not obtain across all taxa (Hayes and Barry, 2008).

It is easy to misinterpret the status of an alien population in its early stages of spread. A species ultimately recognized as invasive can often appear non-invasive at that time. Few individuals are encountered, and population growth and spread can be difficult to detect during this “lag-phase”, when population sizes are doubling but appear quiescent because of low total numbers. Slow doubling rates, which are typically associated with slow maturation rates and long life spans, can make a species appear non-invasive for one or more human lifetimes. Because it is difficult to perceive the growth pattern without explicit measurement and quantification, complacency about such a species can be easy. Consequently, management responses are frequently delayed until the invasion is logistically difficult or impossible to stop. This has the practical effect that many alien invasions become managerially dichotomized into two stages: (1) “it’s not a problem”, and (2) “it’s too late to do anything”. The middle ground of the lag phase, when human control activities could prove most effective, is often squandered because we are maladept at recognizing it. This seriously undermines efforts to meaningfully control many invasive species and has been a frequent problem for herpetological invasions (see Chapter 4).

An invasion will progress more rapidly if it involves many separate populations rather than only a single one (Moody and Mack, 1988; Mack and Moody, 1992). This can occur either because a species is introduced independently to multiple localities or because a single invasive population further expands to multiple sites with human help. As multiple populations become established, each expands at

(relatively) the same rate, making total rate of new range expansion proportional to the number of populations. This has tremendous practical implications for controlling invasive species. When tackling an invasion, managers often deem it best to attack the largest population(s) first. Instead, modelling indicates that limiting the number of new localities infested and eliminating small satellite populations should be higher priorities (Moody and Mack, 1988).

Impacts

It would probably be fair to say that greatest research progress in the past 20 years has been had in a broader elucidation of the numerous impacts that invasive alien species can impose. These impacts are remarkably variable and include extinctions of species, biotic homogenization, disruptions to food-webs, changes to primary productivity of ecosystems, changes in soil formation, alterations of community structure, wholesale conversion or replacement of ecosystems, changes in nutrient-cycling dynamics, collapse of fisheries, degradation of watersheds, promotion of increased fire frequency and extent, increases in erosion and flooding rates, losses to agriculture, damage to human structures, disease epidemics, and degradation of human quality of life (Greenway, 1967; Ebenhard, 1988; van Wilgen et al., 1996; Wilcove et al., 1998; Mack et al., 2000; Pimentel et al., 2000, 2005; Mooney and Cleland, 2001; Pimentel, 2002; Mooney, 2005; Towns et al., 2006; Binimelis et al., 2007; Charles and Dukes, 2007; Reaser et al., 2007). Examples of these impacts are too many to enumerate but can be found by the score in the articles just cited or in the scientific and popular books cited at the beginning of this chapter. Hence, I will not discuss this issue in detail but will merely give one brief example from the non-herpetological literature to illustrate both the novelty, unpredictability, and damage that are so frequently wedded in invasion biology.

The comb jelly, *Mnemiopsis leidyi*, a zooplankton feeder native to western Atlantic estuaries, was introduced to the Black Sea around 1982. It quickly formed extremely dense (1.5–2 kg/m²) biomass, and zooplankton communities declined 15–40 fold (Kideys, 1994). As a result of jelly predation on their food and fry, anchovies (*Engraulis encrasicolus*) and other planktivorous fish species declined dramatically, with fisheries collapsing by 4–40 fold, depending on the fish species and country (Kideys, 1994, 2002; M. Williamson, 1996). Anchovies and other fisheries had been an important source of human protein for communities around the Black Sea, so it is not difficult to imagine the economic hardship and decline in quality of life occasioned by this introduction. It is estimated that fisheries profits declined from US\$17 million/year before the invasion to US\$0.3 million afterwards (Knowler and Barbier, 2000). This cost does not include the estimated several thousand lost jobs as well as secondary effects on economically linked enterprises (Knowler and Barbier, 2000). The jelly population happened to be brought under control a few years later by the inadvertent but fortuitous introduction of a second comb jelly, *Beroe*, which feeds on *Mnemiopsis*. This led to recovery of some

ecosystem values and of the anchovy fishery (Kideys, 2002). *Mnemiopsis leidyi* has subsequently been introduced into the Caspian Sea as well, and can be found there in plague proportions at densities $>2,000/m^2$. Similar ecological and economic damage followed: fisheries losses to Iran alone have exceeded US\$125 million (Kideys, 2002; Stone, 2005). Unfortunately, the salinity of the Caspian Sea is insufficient to support healthy populations of *Beroe*, thus the control of *M. leidyi* happily effected in the Black Sea looks unlikely to succeed in the second case.

It is hard to decide with this example which has a stronger grip on the imagination: the novelty or the horror of an obscure invertebrate decimating the Black Sea and Caspian Sea ecosystems. This example is especially instructive because at the time of ballast-water discharge, no one would have predicted that the “mere” comb jelly thus released would lead to such devastating impacts within a few years. A similar unpredictable scenario applied to the introduction of brown treesnakes, *Boiga irregularis*, to Guam. The literature is replete with similar examples where the ecological damage attending an introduction would have been equally impossible to predict. In other cases, negative impacts were perfectly predictable but ignored until too late, such as with the introduction of coqui frogs (*Eleutherodactylus coqui*) to Hawaii or predatory snails (*Euglandina rosea*) and flatworms (*Platydemus manokwari*) around the islands of the Pacific.

Despite an abundance of impacts on humans and their economic activities, economic costs from invasive species have only infrequently been measured, except for some agricultural pests. Economic costs include those resulting from damage, control, research, defensive prevention, and foregone economic opportunities that attend the irreversibility of pest invasions, which is especially difficult to measure (Perrings et al., 2005). Even when economic impacts are recognized, monetary estimates are usually lacking. However, this is beginning to change, and even conservative estimates have found the monetary costs of invasive species to be staggering. As one example, Pimentel et al. (2005) conservatively estimated the total cost of invasive species to the economy of the United States to exceed US\$120 billion/year. Proportionately similar costs no doubt apply to many other economies. Such estimates (see Pimentel, 2002; McNeely, 2005; Perrings et al., 2000, 2005; Pimentel et al., 2000, 2005) rarely involve reptiles or amphibians, but what data are available for those taxa are presented in Chapter 3.

The impacts discussed above and emphasized in the literature are all of practical concern to one degree or another, affecting humans directly or affecting the ecosystems that support us and innumerable other species. There is one more impact that I wish to mention that is of less obvious practical import and is virtually ignored in the literature on alien species. This is loss of beauty. That such an aesthetic impact exists might seem counterintuitive inasmuch as introductions via the pet trade and deliberate introductions due to personal fondness for an animal's appearance are so frequent (see Chapter 2). After all, an assortment of lizards, birds, and many other species are lovely, widely kept as pets, and sometimes released for that reason. How could introductions motivated by an appreciation for these animals' beauty lead to loss of beauty? Does this not present us with a paradox?

No. The seeming paradox appears merely by forgetting that the biological world is hierarchically arranged into different levels of organization and that the beauty of individual animals is not the threatened beauty that I am discussing. The introduced animals themselves retain their individual beauty but by wrenching them out of their evolutionary contexts and arbitrarily placing them in a strange land the beauty of that recipient land, its native fauna, and the evolutionary history of the transported species become compromised. It is this beauty of higher organizational levels – particularly that of unique species, communities, and ecosystems – that is threatened or lost. This may sound odd to those accustomed to thinking of beauty as inherent in sensory-accessible structures, such as particular plants, animals, or human artifacts. In what does this more abstract form of beauty consist? How can one speak of the beauty of species, communities, and ecosystems? They do not have color, pleasing shapes, symmetry. If not, then what is threatened with loss by the movement of non-native species?

That which is lost is the beauty inherent in the biological systems and relationships evolved under unique historical regimes of migration, competition, and evolutionary accommodation. These unique histories have led to the evolutionary development of unique floras and faunas in different parts of the world. These evolved biotas include species, each with a unique combination of adaptive features allowing it to survive in its own particular slice of the world; communities of co-evolved and co-accommodating species creating geographically unique assemblages of life forms; and the ecosystems whose mix of unique communities, climatic regimes, and topography impart to landscapes their specific distinctiveness and appeal. I suggest that the distinctive co-evolved, unique beauty of each of these systems is besmirched by the introduction of alien species – much as a beautiful beach or coastline may be impaired by an oil spill. Or perhaps more aptly, the facile pollution of these self-generated biotas by human introductions is equivalent to splattering the canvases in the Louvre with day-glo paint: the structural integrity of the canvases may not be marred, the added colors may be beautiful, but the aesthetic integrity of the artworks is thoroughly violated. The difference, of course, is that the impact of an oil spill lasts for mere years, vandalism of a painting may be rectified by careful restoration, but alien invasions are most usually irreversible and irreparable.

I recognize that arguing loss of beauty due to alien introductions may leave many readers unimpressed. Beauty is frequently thought of as an interpretation or response to a sensory perception, and we have gained some understanding of human judgement of nature's beauty as measured by perceptive factors such as vegetative color, shape, and structure (Lohr, 2007). But recognition of common themes to sensory evocation of beauty is a far cry from arguing on behalf of the beauty of ecological relationships, evolutionary consequences, and biological uniqueness, all of which comprise a far more derivative, conceptual, and abstract aesthetic. Yet, that this form of beauty should be abstract or invisible to many people hardly serves as a compelling argument against its existence – any more than the failure of most humans to perceive abstract mathematical beauty argues against its existence. Lack of a broad appreciation for this ecological/evolutionary

aesthetic may simply signify that its appreciation requires a degree of knowledge and/or training that most people have, to date, proven uninterested or maladroit at acquiring. Or such appreciation may be more widely felt but rarely articulated. In either case, lack of human interest, talent, or clear articulation do not prove such beauty to be absent or unattainable. They merely show its appreciation (or articulation) to be rare among members of our current societies – much as appreciation of literature was rare during the Middle Ages or the Renaissance and appreciation of Fourier transformations, Hamiltonian geometry, and fractals non-existent. Our current cultural status may be such that most people can do no better than respond to the sensory impact of an individual plant, animal, or landscape. This is not an ideal situation, of course, inasmuch as many people will rave about the “beauty” of highly invaded landscapes that are nothing but ecological kitsch – such as typify, say, most of lowland Hawaii. However, even this aesthetic appreciation is a tremendous advance over that available in the West in, say, the Middle Ages, when wild landscapes were viewed with fear (Oelschlaeger, 1991) and a relatively small contingent of plants and animals were valued for strictly utilitarian purposes. It is ironic, of course, that many educated people today consider knowledge of art or literature a *de rigueur* sign of sophistication while at the same time so many of them are the equivalent of ignorant hayseeds when it comes to appreciating the beauty of the evolved biosphere upon which their lives depend. But, then, irony is hardly a novel discovery in the human condition, and one presumes this situation will improve as human understanding and aesthetics continue to develop and be better expressed.

It will occur to many readers that concern for loss of beauty will sound a pretty trivial concern compared to more “practical” issues such as ecological degradation and economic loss. And at some level that may be true. But I would caution against unthinking recourse to the philosophy of economism, which attempts to reduce so much of human life to mere economic concerns and to ignore or dismiss those facets of experience that are not so readily reduced. We humans inveterately view ourselves as exceptional beings, often to the point of denying our creaturehood and evolutionary history, while clinging to some inchoate notion of semi-divinity. While most of this exceptionalist thinking is misguided, I would suggest that two features that truly are remarkable human attributes – possibly, but not necessarily, unique in our evolved biosphere – are our predilection for ethics and our strong response to beauty. It is these features – not language, tool-making, opposable thumbs, or bipedal gait – that so clearly demarcate human life from that of our fellow animals and which have historically served to remove us from Thomas Hobbes’ pessimistic vision. They provide meaning to our lives and serve to lift them from the realm of mere selfish, resource-grubbing existence. Under those circumstances, I think that loss of beauty is not a concern we can afford to lightly dismiss, even if the rather abstract beauty under attack should not yet be widely appreciated across our species. Hence, I suggest that in allowing our native ecosystems to be carelessly vandalized by alien introductions we ensure the aesthetic and spiritual impoverishment of ourselves and future generations.

I explain this impact in some detail because even in those cases in which an established alien population does not cause economic or ecological damage, it will always incur an aesthetic cost. So far as I know, no consideration of aesthetic damage from alien introductions appears in the invasive-species literature, whether for reptiles, amphibians, or any other taxon. This probably reflects the discomfort that many biologists would have in discussing such an unquantifiable concept, as well as the fact that social scientists have barely become involved in research on alien species. Nonetheless, I suggest that this is a topic deserving of consideration and future research.

Two remaining points about alien invasions deserve emphasis. First, the effects of invasions are frequently impossible to predict, although ecological mechanisms of impact can often be identified and explained retrospectively. This situation may well remain unchanged: prediction difficulty is a direct result of the inherent complexity of ecosystems formed of the myriad interactions of hundreds or thousands of species with each other and with their changing physical environments. Our knowledge of more than a handful of these interactions in any particular ecosystem is usually rudimentary or lacking entirely, and the large number of possible relationships involved means that an inordinately large number of direct and indirect effects may attend the insertion of any particular novel species into such a system. This complexity has led to invasive-species biology often being a very reactive science – a post-mortem detailing idiosyncratic consequences of invasions that were not or could not have been foreseen. These unpredictable consequences make biotic invasions particularly fascinating and challenging from a scientific perspective, while simultaneously being disconcerting and difficult to address from a management perspective.

A second generality of extremely practical importance is that alien-species naturalizations are usually irreversible. In most instances, once introductions have been allowed to establish, no amount of money or effort can change the situation – much as is widely recognized for other lamentable and irreversible developments such as death, amputation, or the invention of disco music. This irreversibility stems from a variety of biological and social reasons whose applicability to reptile and amphibian invasions will be examined in Chapter 4, but largely reflects the fact that biological entities are self-motivated and not readily susceptible to control. Irreversibility of invasions imposes tremendous economic costs in terms of perpetual damage, control, and foregone economic opportunities (Perrings et al., 2005), a fact not yet widely appreciated by the general public or its political representatives. In those relatively rare instances when it is feasible to reduce or remove damaging alien species, doing so typically involves a rapid response to a new incursion and enormous expenditures of time and money (examples provided in Mack, 2000; Wittenberg and Cock, 2005). High expense is incurred because invasive species will frequently occur in high numbers, be difficult to locate, or both.

Already, thousands of damaging alien species have been introduced worldwide. The number of recognized plant pests alone exceeds 22,000, of which at least 2,000 are environmental pests (Randall, 2002; updated to >28,000 species at

<http://www.hear.org/gcw/>). Hundreds of thousands of potential pests could make the future incomparably worse. This is not merely a reflection of the inherent biological attributes of each potentially invasive species. The invasive-species problem is at its most fundamental level a consequence of varied human values, decisions, and actions (Andow, 2005; McNeeley, 2005), including the commonly taken choice of doing nothing. Adding to scientific knowledge of invasion biology without acting on that information, however, is a sterile exercise. How, then, is our information being used to manage these problems? What prospects are there for improving our responses?

Solutions

A variety of actions may be taken to lessen the frequency of invasion or to reduce the negative impacts of particular invasions. Strategically, one may respond to invasive species at any or all of three stages: by preventing their arrival and establishment, by eradicating newly established populations before they expand, or by mitigating the costs of widespread invasions. Best protection against invasions is had by employing actions (or “screens”) at all three stages because each screen acts independently of the others, and their combined protective effect is multiplicative (Fig. 1.1). Tactical methods useful at each stage should exploit the biological weaknesses of each species; hence, they will vary with species and with the particular environment in which control is being exercised. As a matter of observation and logic it is cheaper, more effective, and therefore more efficient to control alien species earlier in the invasion process than later (see, e.g., Naylor, 2000; Touza et al., 2007). A logical consequence of this is that prevention of introductions is far superior in terms of effectiveness, efficiency, and resource use than is reacting to invasions after they occur. Hence, comprehensive quarantine and screening systems to exclude species entry to new areas should form the foundation for any alien-species mitigation program. This paradigm has been applied to some agricultural pests, but the approach is still new and little applied to environmental pests, except in New Zealand and Australia. Should alien pests breach the quarantine barrier, the most cost-effective means of mitigation is to discover and eradicate newly established aliens while populations remain small. If successful, this avoids the large costs of perpetual control for widespread species. For environmental pests, long-term control is usually applied only in relatively small areas of especial ecological significance, making it an inherently limited solution. Important economic pests may elicit broader treatment. Clearly, avoidance of perpetual management and its attendant costs is to be preferred, so prevention of species incursions or their rapid identification and eradication prior to spread are strategically the most sensible tools of choice. Their competent application avoids the difficulty and cost of long-term control operations and the unpredictable hazards attendant upon allowing alien species to become established. Nonetheless, no single prevention screen will be 100% effective, and sensible invasive-species mitigation programs utilize all three

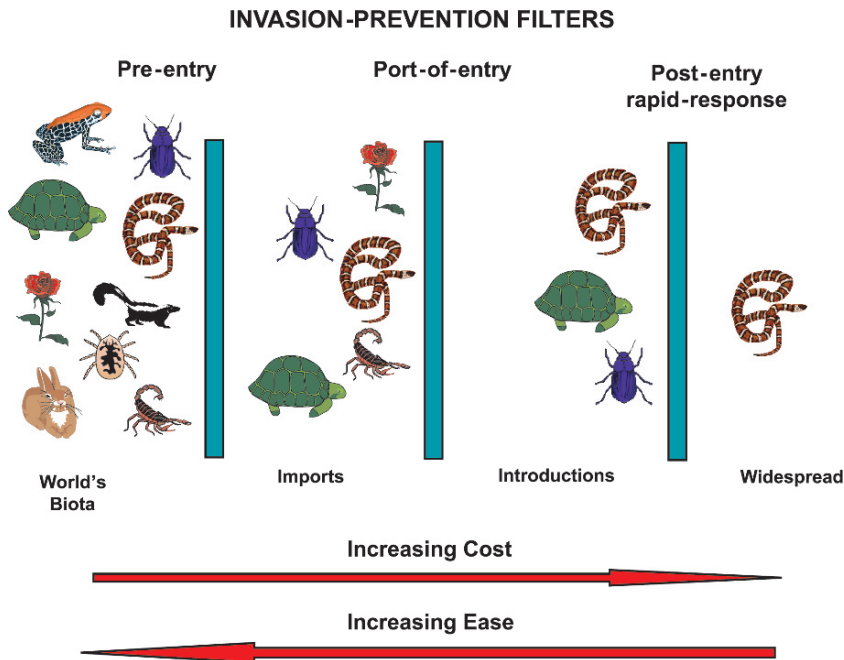


Fig. 1.1 Illustration of the multiplicative protection provided by erecting programmatic barriers to the spread of invasive alien species at the three stages of pre-entry (preventing transportation), port-of-entry (preventing introduction), and immediately post-entry (rapidly eradicating new incursions). The cost of control is less to intercept aliens early in the invasion process, and the ease of control and effectiveness are also higher. Costs increase and probability of successful prevention decrease as a species wends its way through the invasion process

approaches. I will briefly consider topics relevant to each stage of response activity, including certain limitations of each, because these highlight the need for comprehensive response programs that do not overly rely on one method alone.

Strategic Considerations

Before considering different response screens, a few cross-cutting strategic considerations merit consideration first. Although the probability that a particular species becomes an invasive pest is low, the costs if it does so can be very high. This combination of low risk of invasion with high potential hazard can easily skew human perception of risk (Perrings et al., 2005), making sensible assessment of management options problematic. The history of alien-species invasions serves as testimony to the ease with which this skewed judgment operates. The need for the future is to minimize the risk of additional introductions and effectively manage the numerous pests that have already invaded. For reasons given above, risk of

future invasions is difficult to quantify. Government agencies have instead often taken a qualitative approach in which risk probabilities at each step (introduction, establishment, and spread) are qualitatively categorized by a panel of experts as “high”, “medium”, and “low”. The product of the constituent probabilities for invasion is then scored as that of the lowest component (Simberloff, 2005). A similar assessment may be done for species hazard, and the value of the hazard risk is then multiplied by that for invasion risk to produce an overall assessment value (Simberloff, 2005).

There are many problems with the approach just outlined, including its vulnerability to political tampering, narrowly circumscribed taxonomic ambit, practical inability to assess every taxon of interest or concern, presumption of safety for species whose biology is poorly known, and inability to predict consequences for species not yet introduced anywhere (Simberloff, 2005). Hence, one must be cautious in placing too much confidence in the results of such assessment, and different means of assessing invasion impacts may sometimes be preferred (Binimelis et al., 2007). However, such qualitative assessments still have value. The important point about consideration of risk is the conceptual framework that it provides in thinking about how to reduce the future burden of species invasions. Dividing the invasion process into separate steps allows for clearer thinking about the biological and human factors operating at each stage and how those factors might be altered to best reduce invasion probability. This can allow for better decision-making about when and how to respond to alien species. For example, increased international trade increases the risk of introduction of unwanted aliens in a cumulative fashion. This trend is not likely to change in the near future, so responsible governments need to recognize the looming future risk and respond with prevention systems commensurate to the task.

One means of managing the high uncertainties involved in predicting invasiveness and costs is the adoption of a precautionary approach. This principle, as concisely put by Perrings et al. (2005), holds that “where the effects of some activity are uncertain but are potentially both costly and irreversible, society should take action to limit those effects before the uncertainty is resolved.” The justification for such an approach is both that the costs of foregoing preventive action are likely to outweigh the costs of doing so and that the burden of proof for potentially damaging activities, such as importing alien species, lies with those benefiting from the activities. Fundamentally, it is a statement that scientific uncertainty should not be allowed to prevent society from taking action to avoid potential risks (Andow, 2005). It will come as no surprise, however, that the uncertainties involved in understanding species invasions allow for plenty of political bickering over relative costs and benefits. Consequently, although invasion biologists and managers have long argued for the application of a precautionary approach to alien-species management, presumptions about what constitutes precaution, safety, and risk vary tremendously among countries, government agencies, and international treaties (Andow, 2005). In at least one instance, New Zealand’s Hazardous Substances and New Organisms Act of 1996, the precautionary principle has been codified into law and is discharged by that nation’s Environmental Risk Management Authority

(see <http://www.biosecurity.govt.nz/>). Elements of that approach are applied in other jurisdictions as well (e.g., Australia, South Africa). Most countries, however, have avoided addressing the issue and lack any formal process for systematically responding to invasive alien species that goes beyond ad hoc reaction.

Prevention

Successful prevention requires a clear understanding of how the organisms in question are transported and what parameters determine pathway success rates. For species that are introduced unintentionally as hitch-hikers on commercial goods – such as many insects, other invertebrates, and agricultural weeds – inspection and quarantine of arriving goods, containers, baggage, and vessels to ensure they are pest-free will theoretically suffice to keep these pests out. For organisms that are deliberately introduced – such as pets, biocontrol agents, and food species – development of screening systems to assess the likelihood of the species becoming established or becoming invasive are more appropriate. Species deemed of high risk are prohibited from import; species of uncertain hazard are also typically banned pending further assessment to clarify probability of pestiferousness.

Quarantine inspection is typically directed to those articles considered at high risk of harboring unwanted pests because the huge volume of traded material makes it impossible to search all arriving items. Risk can be assigned to particular commercial goods, types of packing material, types of vessels, or to arrivals from particular source areas; it may be estimated using analysis of past interception records, random searches of selected goods and baggage, or from “blitz” inspections that comprehensively search an entire shipment of goods or passengers. Most high-risk materials will receive an inspection at the port-of-entry that may vary in thoroughness depending on the resources available. High-risk commodities may be held in isolated quarantine facilities to determine whether they are free of pests; this is most often done for living commodities, such as pets and horticultural plants. As personnel and resources are available, effort may be directed to articles of lesser risk. For governments having the resources, certifying the pest-free status of commodities by examining them prior to export from the country of origin can be a means of improving cleanliness of imported materials. But this option is typically limited to inspection of agricultural commodities for known, high-risk pests. Practical control methods at this stage typically involve inspection for pests, treatment of articles suspected of harboring pests, and exclusion of particular commodities via trade prohibition (Wittenberg and Cock, 2005). Treatment methods for contaminated plant produce are briefly reviewed by Hallman (2007); several of these methods are useful as well for invasives that do not target plants.

Two weaknesses characterize most inspection programs: (1) only a handful of alien species are targeted quarantine pests, with the remainder ignored or allowed

entry even if detected, and (2) resources are inadequate to provide comprehensive inspection, even were a larger array of alien species targeted for quarantine. In most jurisdictions, the large volume of arriving goods, passengers, baggage, and vessels often precludes meaningful quarantine for more than a handful of unintentionally arriving species. So, current quarantine inspection programs are generally far from ideal. A more promising approach would be wider application of vector science – understanding and managing the motives that create the pathways of introduction and the specific physical means of introduction (or vectors) that transport species (Carlton and Ruiz, 2005). The benefits of a vector-analytic approach are that it can simultaneously work to prevent the introduction of multiple species carried by the same vector and it is likely to be economically efficient by prioritizing those pathways and vectors accounting for the greatest numbers of introductions or invasions. Its intent is to reduce viable transport of all alien species associated with particular vectors or pathways instead of just a limited list of already-identified invasives. This approach requires identification and quantification of pathways and vectors as well as the development of tactical means to limit successful transport by those means. Vector science is relatively new but its recent application includes treatment of ballast water and placement of some restrictions on the import of raw logs for timber. Detailed studies of pathways and vectors are not available for most taxa or commodities, and much of what commodity data are available sit unpublished in government files. But much of what understanding is recently available is summarized in Carlton et al. (2003).

Currently, most countries adopt a short list of known invasives that they attempt to keep from their shores, and most of these are species liable to accidental introduction. These species are almost always pests of agricultural concern and are a very small subset of all known or potential invasives. Ideally, one would like to be able to screen any alien species for potential invasiveness and use that information to decide whether to allow or ban its deliberate importation. Such screening systems would require a methodology that can reliably identify and exclude most invasive species, approve most useful or non-threatening species, and limit the number of instances of uncertain status that require further assessment. Australia has developed screening protocols to meet these goals for plant and animal introductions (Bomford and Hart, 1998; Pheloung et al., 1999; Walton et al., 1999; Bomford, 2003; Bomford and Glover, 2004), and the plant protocol has been adopted for use in New Zealand with minor modifications (Williams et al., 2002) and found applicable to a variety of other locations (Gordon et al., 2008). These protocols are based on assigning numerical scores to a variety of biological traits for a species, summing the scores across all assessed variables, and using this summary score to decide whether to allow importation (low scores), prohibition (high scores), or further assessment (intermediate scores). By use of such a simple system, it has been determined in New Zealand that most invasive species of plants can be kept from entry, most useful non-threatening plants can be allowed safe entry, and a small proportion of species fall into a narrow numerical zone of uncertainty that requires further study prior to making a definitive decision. The system is conceptually simple, evidentially explicit, and objective, making it transparent to

affected stakeholders. It has also been shown in Australia to be easily and cheaply implemented. The advantages of such a system over the current, widespread use of limited “black” lists prohibiting known pests is that a far larger pool of species can be explicitly evaluated for invasiveness and that a “white” list of safe species is simultaneously generated, providing a measure of regulatory stability and predictability useful when making economic decisions involving importation. The system has also been shown to not only protect natural resources but also to generate net economic benefits by exclusion of harmful pests (R.P. Keller et al., 2007).

Eradication/Control

When aliens slip through these prevention screens, the next-best means of avoiding damage is to identify a new incursion as rapidly as possible and target it for eradication. For eradication to be successful requires that several conditions be met: proper planning, socio-political commitment, a removal rate exceeding replacement rate, that all individuals be placed at risk, and prevention of reinvasion (Bomford and O’Brien, 1995; Clout and Russell, 2006). Systematic targeting of new incursions requires having in place a systematic survey program and dedicated, permanently funded staff to respond to new escapees. The former better guarantees identifying new incursions before they have proliferated too far. Doing this successfully requires sensitivity to the lag-phase phenomenon. Permanent staff are needed to ensure that eradication measures continue for the length of time required to ensure success, which can vary tremendously, depending on the species: large conspicuous animals may often be eradicated in relatively short order; plants will produce a seed bank that requires repeated control operations to remove all newly germinated plants to prevent additional reproduction. Small and secretive animals, such as most reptiles and amphibians, may be virtually impossible to eradicate once established because they are difficult to detect and because feasible control methods are frequently lacking.

Explicit use of eradication measures against incipiently established aliens is of relatively recent occurrence and is currently limited, though expanding, in scope. This method has proven successful against environmental pests in New Zealand, Australia, and Hawaii and is becoming common procedure in those jurisdictions. Invasions successfully prevented in this manner are varied, but I will give one example to show what is achievable with rapid, competent response to new incursions. Perhaps the most impressive instance is the eradication of the mussel *Mytilopsis* sp. from Darwin Harbor, which was completed within one month of its detection in three marinas, even though it occurred at densities as high as 23,650 individuals/m². This carefully planned and orchestrated operation involved immediate legislative action to authorize control activities, surveys of hundreds of ships and man-made structures to delimit the range of the infestation, quarantine of three infested marinas, laboratory trials of control methods, chemical treatment of the infested areas totalling approximately 20ha of harbor, chemical treatment of

interior plumbing on all quarantined vessels, public education to gain community and stakeholder support, and monitoring of the treated areas for one year (Bax et al., 2002). As noted, successful eradication was achieved within one month of first detection of the incursion, but success was not declared until mussels had remained undetected for one year. Most eradication operations neither proceed this quickly nor have a need to because most invasive species lack this mussel's capabilities for explosive growth. But this example demonstrates what may be achieved by rapid response against difficult odds when such an operation is approached with commitment and competence. In marking that achievement, Australia's Northern Territory has set a useful standard against which other jurisdictions may measure their own response efforts.

Should an invasive alien species be allowed to spread widely, it is usually impossible – or at best very expensive – to eradicate it. Under these circumstances, one is faced with the prospect of perpetual control to mitigate the worst effects of the alien invader. The means of effecting control and mitigating damage will vary depending on the taxon, habitat, and management goals, but all such efforts need to be carefully defined, planned, and executed in order to meet those goals. Mechanical and chemical control methods are the most widely utilized tactical tools, and numerous options are available, their application and effectiveness depending on the target (examples given in Kraus, 2002a; Wittenberg and Cock, 2005). Although these tactical methods form the backbone of most control operations, more biologically sophisticated techniques, such as removal of disturbance regimes that promote proliferation of the pest, or alteration of habitat to remove refugia for invasives or to provide a competitive edge to natives, can also be used against some invasive pests.

Introduction of natural enemies – either predators or parasites – from a pest's native range has been a frequently used control option and is termed “classical biocontrol”. Biocontrol has most often been applied against plant or invertebrate pests, and these efforts have frequently met with some degree of success in controlling the invasive pest. When properly applied, biocontrol is often the only hope for effecting large-scale control against many wide-ranging plants and invertebrates, and some programs have reduced the target species to such low numbers that it no longer acts as a pest. However, biocontrol programs have also led to unintended disastrous consequences for non-targeted native wildlife (Howarth, 1990, 1999; Louda et al., 2002). This has occurred primarily because some released control species proved to have wide dietary ranges that went unrecognized because of poor (or no) host-specificity testing prior to their release. Attempts to use biocontrol against vertebrates have almost always been ineffective because of lack of host specificity in vertebrate predators and parasites. Use of vertebrates themselves as biocontrol agents has often been disastrous because most vertebrate predators have broad diets and do not restrict their dining to the target species. Because early biocontrol efforts often created unintended impacts on non-target species these programs are now often conducted with extensive testing prior to release so as to ensure that such collateral impacts do not occur. Nonetheless, monitoring of post-release outcomes remains insufficient (Simberloff and Stiling, 1996), and there is still scope for improving the application of this important control tool.

Because control actions taken against invasive pests can themselves have potentially broad ecological impacts, due deliberation and care must be exercised to ensure that such impacts are minimized or avoided. For example, unintended damage to native wildlife may occur because some natives may now use invasive species – such as using invasive plants for food or refugia – for lack of other options. Such conflicts arise as a direct result of the tremendous degree to which human activities have modified the world. This is not to say that large control operations against invasive species should be abjured, merely that they need to be thoughtfully planned and implemented so as to avoid creating additional problems for the biotas or resources they are intended to protect.

Long-term management and control of ineradicable pests thus can be a complex undertaking with diverse ramifications. Typically, benefits are believed to outweigh costs where the goals of the control effort are clearly defined and lead to protection of high-value resources, e.g., biodiversity or agricultural sites of high value. These issues and the complexities involved are treated in greater depth by Wittenberg and Cock (2001) and Courchamp et al. (2003), which should be consulted for more thorough treatments of management topics. De Wit et al. (2002) provide an excellent example of how to conduct an explicit cost/benefit analysis identifying best control options for a widespread invasive. It is worth emphasizing, however, that although range-wide eradication of widespread invasive pests is typically unachievable, discrete geographical units, such as islands, may be liable to removal of invasives and sustained as pest-free. For these instances, considerable progress has been made in developing tactical methods and operational strategies for the eradication of invasive pests from increasingly large areas. A recent sampling of such work can be found in Veitch and Clout (2002), and comprehensive summaries of operations against certain pests (Nogales et al., 2004; K. Campbell and Donlan, 2005; Howald et al., 2007) or for certain geographic areas (B.D. Bell, 2002; Burbridge and Morris, 2002; Ebbert and Byrd, 2002; Merton et al., 2002; Tershy et al., 2002; Clout and Russell, 2006) are also available. With respect to reptiles and amphibians in particular, however, tactical control methods are poorly developed, although mechanical, chemical, and habitat-modification tools have all been attempted. These examples will be discussed in Chapter 4.

History of Research on Alien Reptiles and Amphibians

Although impacts from some alien invasions have been recognized since the late 1800s (cf. Elton, 1958), it wasn't until rather recently that problems associated with reptile and amphibian invasions began to be noticed or documented. Hence, while Ebenhard (1988) could devote a 107-page monograph to the ecological impacts of alien birds and mammals, mention of reptiles and amphibians is absent from Elton (1958) and Mooney and Drake (1986). Similarly, the cane toad (*Bufo marinus*) is the only herpetological species to appear in Groves and Burdon (1986), and it merits only passing mention. This delayed concern for alien reptiles

and amphibians probably stems from the interaction of two factors. First, most of these species are cryptic and insectivorous, making their true densities difficult to perceive and obviating any direct impact on humans or their economically important domesticated animals. Hence, alien reptile and amphibian populations are easy for most people – including most scientists interested in invasive species – to overlook or ignore. Second, much of the literature on these introductions is widely scattered in obscure sources and has previously been unsynthesized (but see Lever, 2003, for a partial, though fairly comprehensive, summary), making it difficult to develop an overall appreciation for the magnitude of reshuffling that has occurred or how it has developed.

This situation has begun to change over the past 25 years. The rapid spread of cane toads across Queensland by the 1970s, combined with anecdotal reports of their poisoning of native wildlife (Breedon, 1963; Rayward, 1974; Covacevich and Archer, 1975), led to considerable government funding to elucidate these effects, understand the biology of the toad, and identify means by which to control it (Tyler, 2006; T. Robinson et al., 2006). The results of this work were a fairly broad understanding of toad expansion, genetics, and parasites within Australia (cf. Appendix A). However, these efforts failed to identify practical control mechanisms, and the toad continues to expand its range rapidly. More effective in bringing attention to herpetological introductions was recognition that the brown treesnake (*Boiga irregularis*) was responsible for the spectacular decimation of Guam's native forest bird fauna (Savidge, 1987a; Savidge et al., 1992), which largely disappeared by the mid-1980s. Lost from Guam were ten species of forest birds, three seabirds, two bats, and six lizards within approximately 40 years (Savidge, 1987a; McCoid, 1991; Rodda and Fritts, 1992; Fritts and Rodda, 1995, 1998; Rodda et al., 1997, 1999a). Three of the birds and one bat were endemic to Guam and are now globally extinct. Two more birds – a rail and a kingfisher – remain only in captivity for the time being. Most of the few native vertebrates that remain on Guam do so at extremely reduced numbers. This was an unanticipated effect from a “mere snake” (J.T. Marshall, 1985), and most ornithologists at the time blamed pesticides or disease for the bird declines (Jaffe, 1994). Consequently, Savidge's evidence and arguments laying responsibility (dare I say) at the feet of the snake were initially dismissed as impossible. The effect of these losses has been a wholesale change in food webs on Guam, with broader ecosystem effects – such as loss of pollinators and changes in vegetation communities – anticipated (Fritts and Rodda, 1998), supported by some data (Perry and Morton, 1999; Ritter and Naugle, 1999), but not yet rigorously tested. Similarly, beginning in the late 1980s, evidence began to accumulate indicating that the bullfrog (*Rana catesbeiana*) is at least partly responsible for the decline of a diversity of native frogs and snakes across the western United States (see Chapter 3). It has also recently been shown to be a likely vector in the spread of chytrid fungus, which has decimated native frog populations around the globe in the past 20 years (Hanselmann et al., 2004; Garner et al., 2006).

The approximately simultaneous acquisition of evidence linking brown tree-snakes, cane toads, and bullfrogs to damage to native species has helped foster a growing awareness of the potential ecological importance of invasive reptiles and

amphibians and has provided an impetus for research on additional species. But this awareness and action still lag well behind that accorded other taxa. Most of this increased activity has merely recorded new introductions, documented range expansions, or provided descriptive autecological information on some populations of naturalized reptiles and amphibians. A growing number of studies, however, has documented additional negative impacts to native biota or to human activities resulting from a variety of invasive herpetofauna (see Chapter 3). Scientists occasionally model predicted range expansions of select taxa based on matching climatic parameters between native and invaded ranges (e.g., van Beurden, 1981; Sutherst et al., 1996; Adrados, 2002; Ficetola et al., 2007a; Urban et al., 2007). There have been regional summaries of herpetological introductions for a few areas (e.g., King and Krakauer, 1966; Bury and Luckenbach, 1976; Smith and Kohler, 1978; L.D. Wilson and Porras, 1983; McCoid, 1995a, 1999; Ota, 1999; Meshaka et al., 2004a; Ota et al., 2004a), and a recent book summarizes some of what is known about particular established species of alien reptiles and amphibians (C. Lever, 2003). A brief overview of some common pathways and impacts of alien herpetofauna has recently appeared (Scalera, 2007a) but is focused on those species associated with aquatic habitats. There have been, however, virtually no studies that test explicit scientific hypotheses about herpetological invasions – most work to date has been simply descriptive.

Little knowledge, too, has been added that would be practically useful for stemming the rising tide of naturalized populations of alien reptiles and amphibians. For example, a couple of brief assessments of introduction pathways for the alien herpetofauna of Florida exist (L.D. Wilson and Porras, 1983; Butterfield et al., 1997), but only one prior study (Kraus, 2003c) has attempted a broad-scale quantitative assessment of this topic, and that was merely an early precursor to the expanded analysis of the next chapter. As for damage from invasive herpetofauna, no rigorous summary of ecological or social impacts from alien reptiles and amphibians has previously been published. Some useful information on impacts may be gleaned from C. Lever (2003), but that book mixes evidence and speculation with little distinction, and there has been much untested speculation about impacts promulgated in the herpetological literature. If informed decisions are to be made on designing prevention systems for alien reptiles and amphibians we need better data on both introduction pathways and ecological, economic, and social impacts. Attempts to predict invasion success have just begun to be investigated for reptiles and amphibians. Rolan (2003) provided an assessment of risk to native amphibians of the United States posed by 24 species of alien amphibians, and Reed (2005) did likewise for an assortment of pythons and boids. Bomford et al. (2005, in press) provided evidence that history of prior establishment, climate match, and phylogenetic relatedness were correlated with establishment success for alien reptiles and amphibians. Rodda and Tyrrell (in press) assessed likely ecological attributes that would favor urban, pet-trade, and invasive herpetofauna, and they concluded that overlap in attributes between these three sets is high. But testing those predictions with empirical data remains to be done. Clearly, efforts to obtain the information necessary to predict invasiveness of alien herpetofauna have just begun.

In short, despite a recent increase in awareness and interest in invasive herpetofauna obtained from damaging experiences in Guam, Australia, and the western United States, the systematic compilation of information needed to make progress in scientific understanding of these invasions or to make informed, practical management decisions about alien reptiles and amphibians has been lacking. It is this information to which we now turn.

Chapter 2

Introduction Patterns

What is the magnitude of alien herpetofaunal dispersal by humans? How are these species being dispersed by humans? Is it mainly the result of intentional actions liable to easy personal control, or an accidental phenomenon of human actions having statistically probable outcomes? Have the mechanisms of introduction been stable through time or varied? Are the same mechanisms important everywhere, or do pathways differ in importance geographically? How successful are alien reptiles and amphibians at establishing populations in the new regions to which they have been transported, and what factors might explain this success?

These are the very basic questions that need to be answered if the phenomenon of reptile and amphibian invasion and its dependence on human behavior are to be understood. A quantitative analysis of these questions is typically referred to as a “pathway analysis” because it assesses the details of how and why species are transported by humans. A pathway analysis is a prerequisite for any informed managerial response to herpetofaunal invasions because it provides the data needed to meaningfully intervene in the first step of that process. Once pathways are identified and their variation clarified, one may then investigate predictive factors (e.g., ecological, economic) that might explain pathway strength and establishment success. This knowledge may then be applied to design measures to restrict pathway strength and success.

Such analysis has historically been hindered for reptiles and amphibians because the requisite literature and evidence remained uncollated. The only prior attempt I know to provide a pathway analysis for reptiles and amphibians is my earlier study (Kraus, 2003c) that was based on approximately one-tenth of the records in the current database. That study was a sampling of those records that I could find in a period of two months and it was acknowledged as suffering from at least a geographical bias. The current database is a sufficiently complete sampling of the literature that it more closely approximates a census of available global information. Hence, I think the limitation of geographic sampling bias present in the earlier study no longer applies to any serious extent.

The database and details on its interpretation are provided in Appendix A. I have used 1850 as a convenient point at which to begin the analyses below because few records reporting introductions precede that date; however, the database includes

mention of all reported dates before 1850 (usually approximate, but sometimes exact) that I could discover.

The database consists of records for 5,745 introductions, representing 675 taxa and 2,141 record entries, where each “species x jurisdiction” combination counts as a separate entry. Numerous entries in the database consist of >1 introduction of a species to a particular jurisdiction. In these cases of multiple introduction, knowing that a species has become established tells us only that at least one of those multiple introductions has been successful. It may be that more than one was successful, but this is usually unknowable and unreported in the literature. Kolbe et al.’s (2004) results using mitochondrial DNA to assess numbers of introductions of *Anolis sagrei* to Florida illustrates one exception to this rule. Hence, for the analyses that follow, measures of success rates necessarily can only consider counts of jurisdictions to which species were successfully introduced and will serve as a (probably slight) underestimate of true establishment success rates. Following this approach, we find that these 5,745 introductions have resulted in 1,060 successfully established populations involving 322 species.

Alien introductions of reptiles and amphibians have increased exponentially since 1850 (Fig. 2.1), with a doubling time of 27.25 years. This growth curve is described by the equation $y = 43.6e^{0.2532x}$, and the fit of the data to this curve is remarkably good ($R^2 = 0.9978$, Table 2.1), indicating that global growth in alien introductions has increased surprisingly constantly through the past 150 years. The dip at the end of the illustrated curve merely reflects the time lag involved in having recent introductions reported in the literature, and it should not be interpreted as indicating that introduction rates have recently declined. For example, in my earlier analysis of subset of these data (Kraus, 2003c), the terminal dip in the cumulative growth curve occurred in the 1990s, not the 2000s.

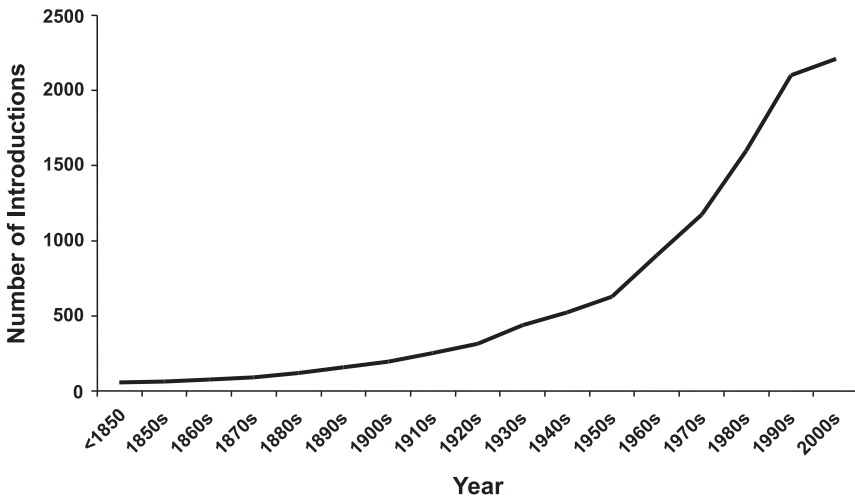


Fig. 2.1 Cumulative growth in global introductions of reptiles and amphibians

It is against this overall exponential increase in alien herp introductions that the following analyses elaborate.

Taxonomic Variation

Introduction and success rates vary considerably among taxa and can be tracked in two different ways. For those data that admit of time-series analysis, frogs have been introduced most frequently, followed by lizards, turtles, and snakes, with salamanders and crocodilians relatively rarely introduced (Fig. 2.2). For each of these taxa, with the exception of crocodilians, growth in introduction rate is exponential, although rates, and therefore doubling times, differ (Table 2.1). Crocodilians have been infrequently introduced and growth in their numbers with time is largely

Table 2.1 Growth rates for herpetological taxa

Taxon	Growth type	Growth equation	R ²	Doubling time (years)
Frogs	Exponential	$y = 17.396e^{0.2310x}$	0.9934	29.9
Salamanders	Exponential	$y = 0.63.47e^{0.3142x}$	0.9746	22.0
Lizards	Exponential	$y = 9.3101e^{0.2424x}$	0.9820	28.5
Snakes	Exponential	$y = 4.7193e^{0.2368x}$	0.9548	29.1
Turtles	Exponential	$y = 4.7072e^{0.2763x}$	0.9843	25.0
Crocodilians	Linear	$y = 3.5667x - 5.5$	0.9760	NA
All taxa	Exponential	$y = 43.600e^{0.2532x}$	0.9978	27.2

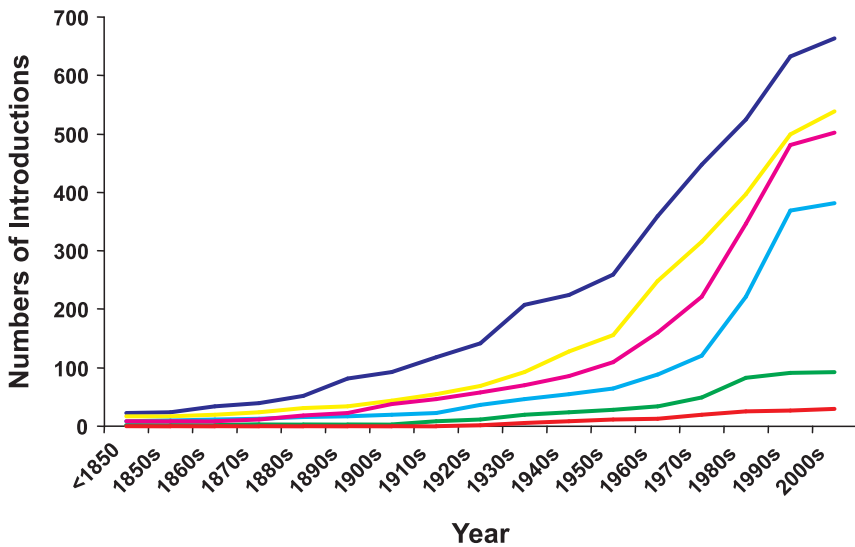


Fig. 2.2 Cumulative growth in reptile and amphibian introductions by taxon. Frogs = dark blue, salamanders = green, lizards = yellow, snakes = blue, turtles = pink, and crocodilians = red

linear. Although frogs and lizards have been introduced most often, the actual rate of increase in introductions through time has been highest for turtles and salamanders (Table 2.1), even though those taxa have not been introduced as often.

Alternatively, instead of restricting analysis to those introductions of approximately known dates, the sum total of all introductions can be examined for each taxon. Doing so indicates turtles to have been introduced far more frequently than any other taxon (Fig. 2.3). However, this total is heavily influenced by the widespread introduction of the common pet turtle *Trachemys scripta*. If this species is removed from the analysis, then numbers of turtle introductions are more in line with those for other taxa (Fig. 2.4). In either event, rates of successful establishment differ among taxa (Figs. 2.3–2.5), with lizards having the highest rate, followed by frogs, salamanders, and snakes. Turtles and crocodylians have very poor overall rates of establishment. If relative establishment success of turtles is calculated excluding *T. scripta*, establishment success rates (Fig. 2.5) increase from 5.7% to 7.7% only.

Most species have only single records of introduction, with the number of species having larger numbers of introductions declining as a negative power function ($y = 419.44x^{-1.8280}$, $R^2 = 0.9077$, Fig. 2.6). Nonetheless, 87 species of reptiles and amphibians have been subject to more than ten introductions each, with *Trachemys scripta* again being the most widely released species, with 1,430 records.

Numbers of introductions per family vary in a similar fashion, with 34 families having been introduced more than ten times and 11 families introduced more than 100 times (Table 2.2). The distribution of numbers of introductions among these families also approximates a negative power function ($y = 6331.5x^{-1.8406}$, $R^2 = 0.8572$). The fit of this equation to the data is compromised by the large number of families having only a few introductions. Restricting attention to only those families

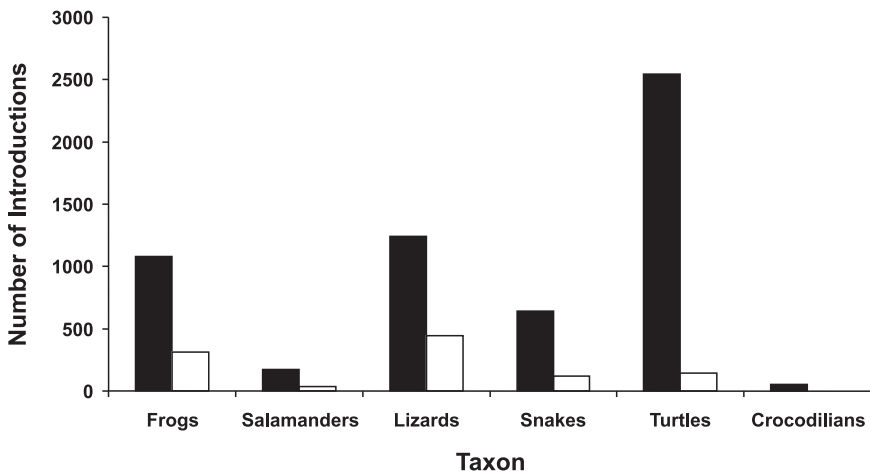


Fig. 2.3 Differences in numbers of introductions among reptile and amphibian taxa. Solid bars are data for all introductions, open bars for successfully established introductions, where establishment is counted only once per jurisdiction

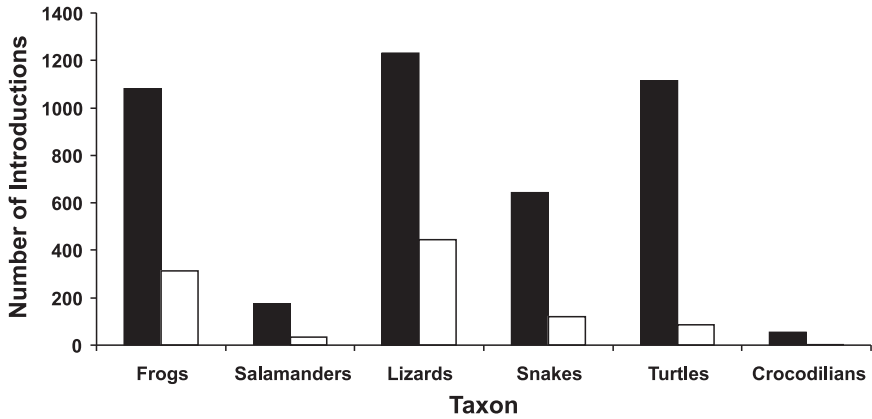


Fig. 2.4 Differences in introduction frequency among reptile and amphibian taxa, excluding the turtle *Trachemys scripta*. Solid bars are data for all introductions, open bars for successfully established introductions, with establishment counted only once per jurisdiction

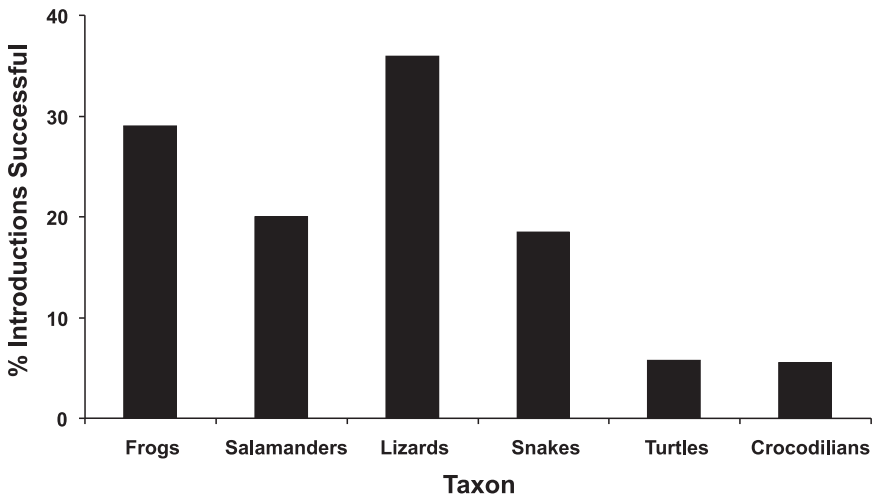


Fig. 2.5 Differential establishment success among introduced reptile and amphibian taxa, with *Trachemys scripta* included in the calculation for turtles

having more than ten introductions provides a better fit to data (Fig. 2.7). Unsurprisingly, ability to successfully establish populations varies among families, and those families having the greatest numbers of introductions are typically also among those having the greatest numbers of naturalized populations (Table 2.3). Certain artifacts characterize some of these results. First, families introduced fewer times are more prone to estimation error; those introduced fewer than ten times are distinguished in Table 2.3. Second, some of those families showing highest success rates do so for unique reasons that do not make them representative. As one example,

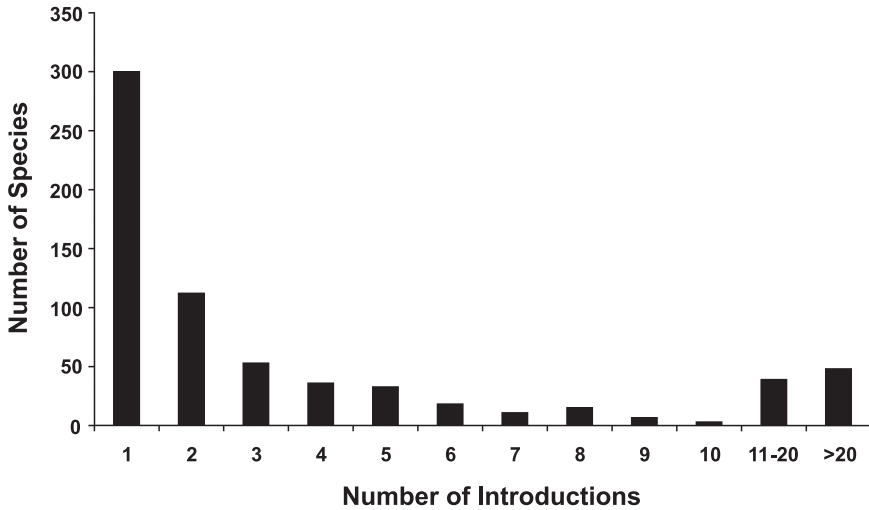


Fig. 2.6 Distribution frequency of minimum number of introduction events among species. The distribution is modelled by the negative power function $y = 419.44 \times x^{-1.8280}$, with $R^2 = 0.9077$

Table 2.2 Numbers of introduction events per taxonomic family. Family numbers correspond to those of Fig. 2.7

Family number	Family	Number of introductions	Family number	Family	Number of introductions
1	Emydidae	2,108	26	Elapidae	34
2	Gekkonidae	503	27	Varanidae	30
3	Ranidae	471	28	Teiidae	22
4	Iguanidae	343	29	Bombinatoridae	16
5	Colubridae	302	30	Microhylidae	15
6	Hylidae	241	31	Pelomedusidae	15
7	Bufo	154	32	Chelidae	14
8	Testudinidae	153	33	Proteidae	13
9	Lacertidae	148	34	Discoglossidae	12
10	Geoemydidae	127	35	Anguidae	9
11	Leptodactylidae	103	36	Kinosternidae	8
12	Pythonidae	86	37	Myobatrachidae	8
13	Scincidae	86	38	Alytidae	7
14	Boidae	84	39	Cordylidae	7
15	Typhlopidae	81	40	Crocodylidae	7
16	Trionychidae	71	41	Rhacophoridae	6
17	Salamandridae	68	42	Cryptobranchidae	5
18	Plethodontidae	53	43	Gymnophthalmidae	3
19	Viperidae	53	44	Helodermatidae	3
20	Chelydridae	50	45	Pygopodidae	3
21	Alligatoridae	45	46	Amphisbaenidae	2
22	Agamidae	43	47	Pelobatidae	2
23	Chamaeleontidae	43	48	Acrochordidae	1
24	Pipidae	37	49	Dendrobatidae	1
25	Ambystomatidae	36	50	Leptotyphlopidae	1

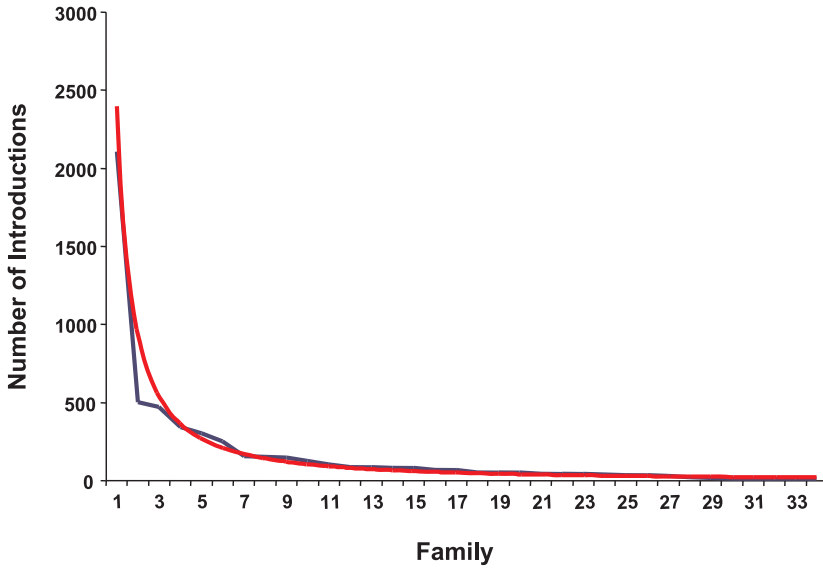


Fig. 2.7 Distribution frequency of minimum number of introduction events among families. Family numbers correspond to those of Table 2.2. The distribution is modelled by the negative power function $y = 2388.6 \times^{-1.3589}$, with $R^2 = 0.9493$

Table 2.3 Variation in establishment success among taxonomic families. Percentages highlighted in bold are for those families introduced more than ten times, making them less likely to be estimation artifacts

Family	Number of successful establishments	Percent of establishment success	Family	Number of successful establishments	Percent of establishment success
Acrochordidae	1	1.00	Myobatrachidae	2	0.25
Dendrobatidae	1	1.00	Lacertidae	36	0.24
Leptotyphlopidae	1	1.00	Varanidae	7	0.23
Typhlopidae	71	0.88	Chamaeleontidae	10	0.23
Rhacophoridae	5	0.83	Anguidae	2	0.22
Gymnophthalmidae	2	0.67	Plethodontidae	11	0.21
Proteidae	7	0.54	Bombinatoridae	3	0.19
Leptodactylidae	54	0.52	Salamandridae	12	0.18
Microhylidae	7	0.47	Hylidae	41	0.17
Agamidae	20	0.47	Discoglossidae	2	0.17
Gekkonidae	226	0.45	Testudinidae	22	0.14
Scincidae	38	0.44	Ambystomatidae	5	0.14
Teiidae	9	0.41	Elapidae	4	0.12
Bufo	58	0.38	Viperidae	6	0.11
Chelidae	5	0.36	Colubridae	31	0.10
Pipidae	11	0.30	Chelydridae	5	0.10
Alytidae	2	0.29	Alligatoridae	3	0.07
Trionychidae	20	0.28	Geoemydidae	7	0.06
Iguanidae	94	0.27	Emydidae	83	0.04
Ranidae	126	0.27	Boidae	3	0.04
Pelomedusidae	4	0.27	Pythonidae	1	0.01

the entire success of the Typhlopidae is due to the success of one species, *Ramphotyphlops braminus*, which is parthenogenic and, hence, far more likely to establish populations subsequent to introduction than any other species in the data-set. As another example, the apparent success of the Proteidae is inflated by the fact that several of its successful “introductions” actually stem from natural dispersal across jurisdictional boundaries from an original introduction. Nonetheless, it is clear that families that have undergone a large number of introduction events can vary widely in their establishment success, a topic that is analyzed in some detail by Bomford et al. (in press) for these same data.

Pathway Variation

Ten pathways accounted for the overwhelming majority of all herpetological introductions, whether pathway importance was measured by total number of introductions involved (Fig. 2.8) or by number of species involved (Fig. 2.9). Of these pathways, six predominate in importance, whether all introductions are considered (Figs. 2.8 and 2.9) or only introductions leading to successful establishment are examined (Figs. 2.10 and 2.11). Hence, the remaining discussion will focus on those six pathways most involved in alien herp movements: biocontrol, cargo, food, nursery, pet trade, and “intentional”. Each of these requires definition prior to continued discussion.

“Biocontrol” refers to instances of species transported and deliberately released in the hopes of controlling some perceived pest, typically a pest of agriculture but sometimes including house pests such as cockroaches. The best-known example of this pathway among reptiles and amphibians is the widespread introduction of *Bufo marinus* around the tropics for the control of a variety of boring beetles that attack sugar cane, *Saccharum* spp. (Easteal, 1981). “Cargo” refers to accidental transport

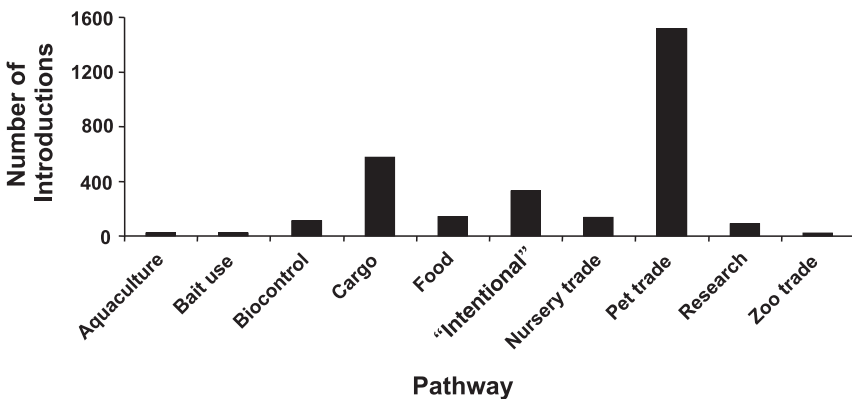


Fig. 2.8 Relative importance of pathways of herpetofaunal introduction as measured by total numbers of introduction events

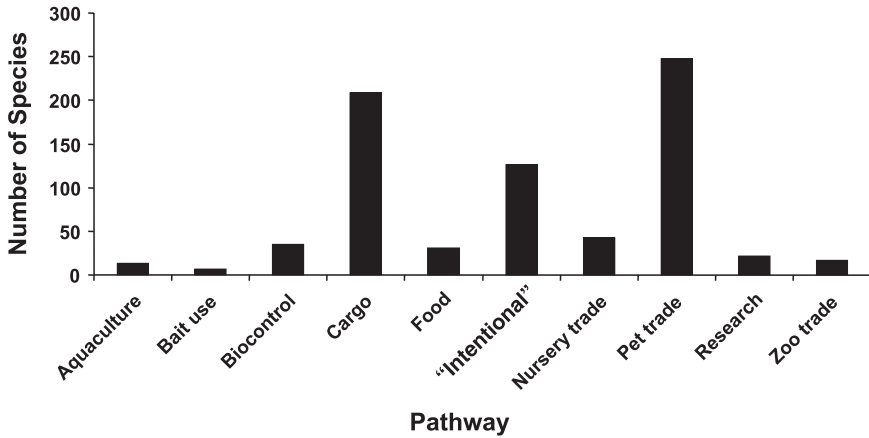


Fig. 2.9 Relative importance of pathways of herpetofaunal introduction as measured by total numbers of species introduced

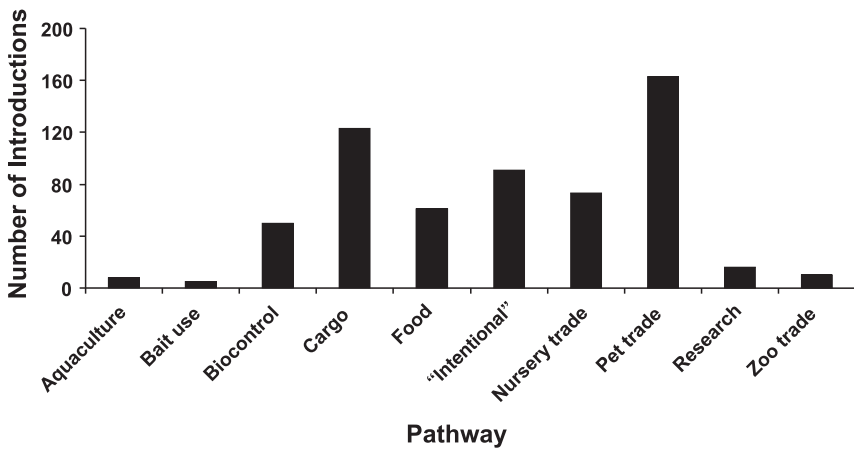


Fig. 2.10 Relative importance of pathways of herpetofaunal introduction as measured by numbers of successfully established introductions, with establishment counted only once per jurisdiction

in packaged or unpackaged goods for human use; it specifically excludes those relatively few noted examples of transport in vehicles per se, although frequently that vehicular movement was for the purpose of transporting cargo. A variety of tropical geckos serve as archetypal poster children for this pathway. “Food” includes those deliberate introductions occasioned by the desire to establish a new food resource in a particular location. Usually, these species, such as *Rana catesbeiana* and *Pelodiscus sinensis*, have been intended for human consumption, but a few species (e.g., *Litoria raniformis* and *Rana esculenta* in New Zealand) were originally introduced for the purpose of establishing a food supply for ducks. “Nursery trade”

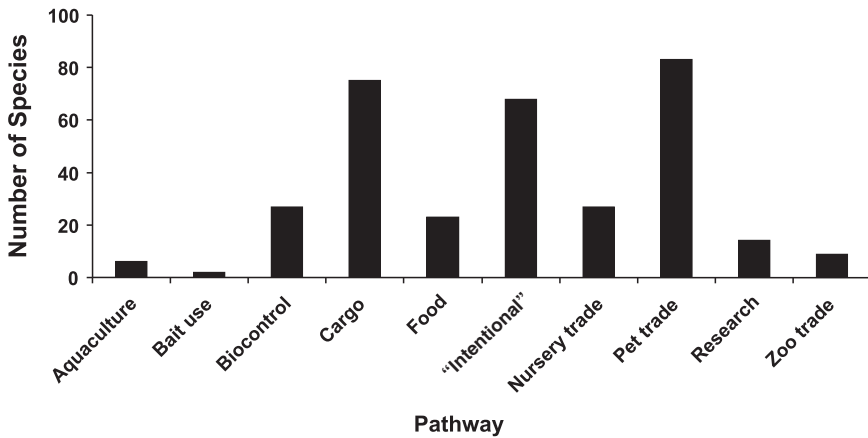


Fig. 2.11 Relative importance of pathways of herpetofaunal introduction as measured by numbers of species successfully established

refers to the trade in live plants, usually for ornamental purposes, although transport of food trees for tropical gardening has also been involved. Clearly, this pathway is a subset of the cargo pathway but has proven of sufficient importance in its own right and presents a qualitatively different set of transport conditions to warrant separate examination. “Pet trade” is self explanatory and includes deliberate releases and unintentional escapes of pet animals, whether the responsible parties were private individuals, retail dealers, or wholesale traders. I generally view the pet-trade pathway as one of intentional introduction even when a particular release may not have been. This is both because the importation was intentional and because the consequence of irresponsible ownership of animals will be the frequent and predictable escape of the deliberately imported pets. “Intentional” as used as a separate category in the figures is somewhat of a catch-all. It refers to what is clearly a deliberate introduction by an individual, but it lacks the precise knowledge of motive that is characteristic of the other deliberate pathways. Most often, introduction for perceived amenity or aesthetic reasons may be vaguely inferred from reports citing this pathway, and there is clearly a close relationship with the motives underlying the pet-trade pathway; however, the precise psychological motives behind the release cannot usually be perceived with any assurance. This is the least well-defined and least satisfying of the pathway categories, but these deliberate releases have nonetheless been an important means of herpetological introductions. Because choice of terminology could be confusing for this pathway vis a vis the sum of all those pathways having an intentional motive (e.g., food, biocontrol, pet trade), when I refer to this specific pathway, I will always enclose it in quotes.

Of these six pathways, the greatest volume of introductions has been via the pet-trade and cargo pathways, with “intentional” introductions trailing those two but still of considerable importance (Figs. 2.8–2.11). The remaining three pathways have also been important but consistently less so in overall numbers.

Contributions of the different taxa to each pathway vary in importance and are generally strikingly different. Indeed, there is a distinctive taxonomic signature for each pathway (Fig. 2.12). Biocontrol efforts involving reptiles and amphibians have focused almost exclusively on frogs. Transportation via the cargo pathway has been virtually restricted to frogs, lizards, and snakes. This is unsurprising inasmuch as these taxa have many species that are small in size and with broad physiological tolerance. Conversely, one could scarcely imagine turtles or crocodilians accidentally hitch-hiking in cargo because their large sizes would make them conspicuous. Similarly, most salamanders would be physiologically susceptible to the dry and hot conditions that frequently accompany cargo transportation. The few instances of their transport in cargo involve shipments of logs or tropical produce. I know of other, unreported instances of salamander transport in christmas tree shipments as well. Transport via the nursery pathway is similarly restricted and for the same reasons. However, frogs form a higher percentage of introductions via the nursery pathway, probably a reflection of the more conducive physiological conditions presented by nursery materials for desiccation-prone amphibians. The food pathway has also had restricted taxonomic representation, being dominated by frogs (mainly *Rana*) and turtles (mainly *Pelodiscus*), although lizards have also been involved. The only pathways that involve all taxa are, unsurprisingly, the pet trade and its close aesthetic cognate, “intentional” introductions. Clearly, this reflects the fact that humans who like and keep reptiles and amphibians are drawn to a wide diversity of taxa and, hence, all groups are subject to some amount of release or escape. Interestingly, taxonomic representation between those two related pathways differs rather dramatically for turtles. This may reflect that the large combined mass required to intentionally start a new population presents

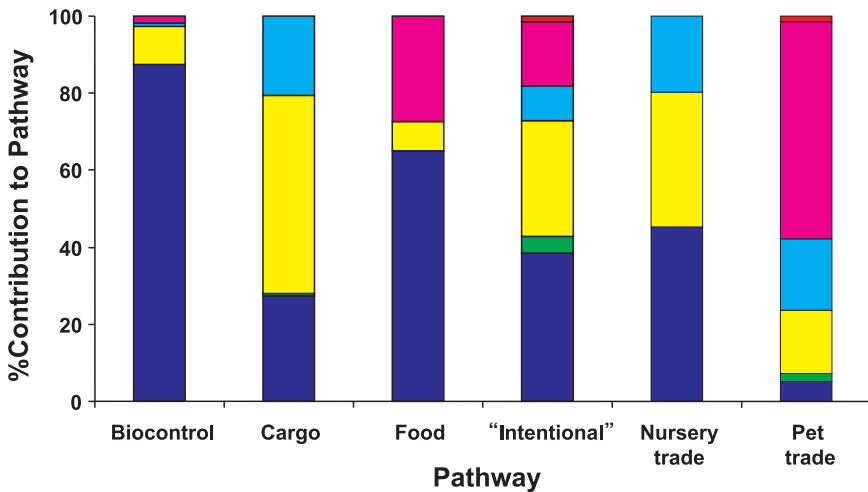


Fig. 2.12 Frequency of taxonomic representation for each major pathway of herpetofaunal introduction. Frogs = dark blue, salamanders = green, lizards = yellow, snakes = blue, turtles = pink, and crocodilians = red

logistical difficulties for most turtle fanciers, being decidedly less easy to arrange than the release of a large number of small frogs or lizards. Conversely, the large number of releases of single or few pet turtles is not logistically burdensome and is correspondingly larger.

One may also upend this matrix of relationships to examine pathway importance for each herpetological taxon (Fig. 2.13). This confirms that crocodilians have been introduced entirely deliberately, that the same is virtually true for salamanders, and that the other taxa have been introduced for a greater diversity of reasons. Frogs and lizards have been introduced via all six pathways, with lizards having a slightly more balanced distribution of introductions across the six pathways than do frogs. Introductions of snakes have involved all pathways except food, and turtles have been introduced mainly through the pet trade and “intentional” pathways, but introductions for food have also been important.

It is of considerable importance to stress that establishment success rates vary across pathways, a result hinted at by contrasting the relative histogram heights in Fig. 2.8 vs. Fig. 2.10 or Fig. 2.9 vs. Fig. 2.11. Examined directly, introductions via the nursery trade, biocontrol, and food pathways have had a higher establishment success rate than those arriving via the “intentional”, cargo, or pet trade pathways (Fig. 2.14). As pointed out earlier (Kraus, 2003c), this is unsurprising because the two deliberate pathways of biocontrol and food have often involved well-funded programs supported by scientific or agency personnel and have often resulted in the coordinated release of many individual animals. This focused, scientifically informed effort with large numbers of propagules has no doubt contributed to making these pathways more likely to lead to population establishment than the other deliberate pathways involving the pet trade and private “intentional” introductions

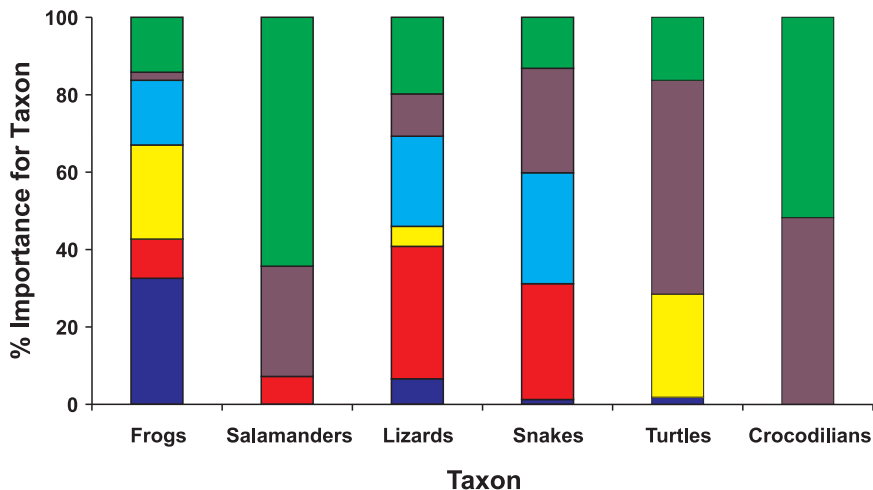


Fig. 2.13 Relative pathway importance for each reptile and amphibian taxon. Biocontrol = dark blue, cargo = red, food = yellow, nursery trade = blue, pet trade = brown, and “intentional” = green

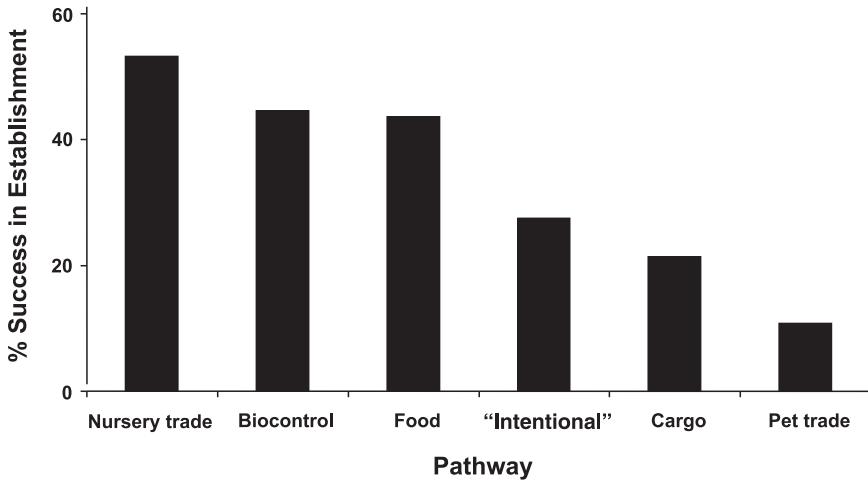


Fig. 2.14 Relative success of each of the major introduction pathways in leading to successful establishment of populations. Relative success is estimated as the count of all jurisdictions to which a successful introduction via that pathway has occurred divided by the sum of all introductions via that pathway

(Fig. 2.14). Given that reasoning, it might be wondered that an accidental-transport pathway such as the nursery trade could result in similarly high success rates. But several factors likely contribute to the high rate of successful establishment for this pathway. First, the pathway involves the wholesale transfer of favorable habitat for the transported animals, greatly increasing their chances of surviving the move. Second, it may be that, on average, greater numbers of animals are involved in nursery shipments than in other forms of cargo because such goods are inhabited by several species of reptiles and amphibians prior to processing for shipment elsewhere. Third, nursery shipments are rather fragile, requiring their transport to be done quickly. Reduced transport time likely increases survivability for stowaways. Fourth, shipment conditions are benign because of the need to keep the plants alive. Lastly, plant shipments are generally made between regions having similar climates, increasing the likelihood that the destination will prove as climatically favorable to the hitch-hiking herpetofauna as was the origin. These seem the salient differences between transport via the nursery and other cargo pathways and likely explain why introductions via other forms of cargo meet with less than half the success rate of nursery introductions (Fig. 2.14).

Lastly, it remains to examine how pathway importance has changed through time. It turns out that these changes have been tremendously important. The “intentional” pathway accounted for most alien reptile and amphibian introductions up through the end of the 1950s (Fig. 2.15). Beginning in the 1950s, introductions via the pet trade began to skyrocket and that pathway has remained the predominant pathway of introduction since the 1960s. During this entire period, the cargo pathway has been of great, but secondary, importance, overtaking “intentional” introductions

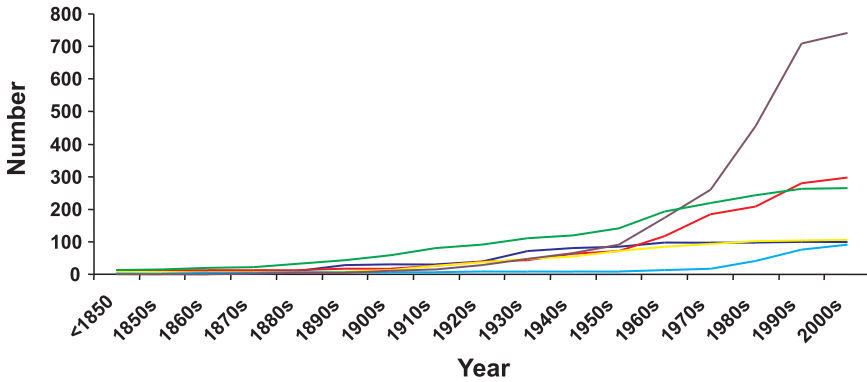


Fig. 2.15 Cumulative growth in reptile and amphibian introductions by pathway. Biocontrol = dark blue, cargo = red, food = yellow, nursery trade = blue, pet trade = purple, and “intentional” = green

in importance in recent decades. Further, the nursery-trade pathway has increased considerably in importance since the 1970s. These patterns can be explained by looking at differences in the individual growth trajectories of each pathway. Each pathway can be well modelled by exponential equations, as was apparent earlier when examining growth in introduction rates for each major taxon (Table 2.1). However, in this case, growth is not exponential for all pathways during the entire time period considered here, and changes in pathway importance over the past 150 years can be explained by the amount of time that exponential growth occurred for each pathway and the magnitude of the exponent involved in that growth (Table 2.4).

Examined in this light, several points are noteworthy. First is that exponential growth can be halted. This is most evident for the biocontrol pathway, which enjoyed exponential growth through the 1960s but has had its growth virtually terminated since then. The food pathway may also be showing signs of decreasing growth since the end of the 1980s, but it is probably too soon to be certain of this. Second, is that the pathway of predominant importance in late 20th century introductions (pet trade) is also that with the highest exponent and, hence, shortest doubling time (Fig. 2.15, Table 2.4). In contrast, the only pathway still clearly growing exponentially whose sum effect (to date) approximates that of the currently non-exponential pathways of biocontrol and food is the nursery trade, which has had the longest doubling time (Table 2.4). Third, is that pathway importance may stagnate for decades and then change rapidly. As one example, the pet trade was a relatively negligible pathway until the 1920s, at which point extremely rapid exponential growth set in. Prior to that point, growth in the pet-trade pathway cannot be modelled by an exponential equation; since that time, the number of introductions via that pathway has doubled every 15.3 years. Similarly, although the nursery-trade pathway has the slowest doubling time over the entire 150-year study period, there was a strong inflection in rate during the 1970s, and, consequently, the equation describing growth in that pathway’s importance across that inflection point (Fig. 2.16) has a higher exponent and much shorter doubling time (Table 2.4).

Table 2.4 Exponential growth rates for each pathway, incorporating all data

Pathway	Period	Time span (years)	Growth equation	R ²	Doubling time (years)
Biocontrol	1850–1969	120	$y = 2.7980e^{0.3000x}$	0.9547	23.0
Cargo	1850–1999	150	$y = 6.0163e^{0.2215x}$	0.9301	31.2
	1890–1999	80	$y = 10.991e^{0.2943x}$	0.9888	23.4
Food “Intentional”	1850–1989	140	$y = 3.0237e^{0.2492x}$	0.9476	27.7
	1850–1999	150	$y = 11.147e^{0.2136x}$	0.9795	32.3
Nursery	1890–1999	80	$y = 42.370e^{0.1766x}$	0.9801	39.1
	1850–1999	150	$y = 2.0542e^{0.1677x}$	0.8193	41.1
	1930–1999	70	$y = 3.6361e^{0.3844x}$	0.8755	17.9
Pet trade	1920–1999	80	$y = 17.367e^{0.4501x}$	0.9949	15.3
Overall	1850–1999	150	$y = 23.709e^{0.2567x}$	0.9948	26.9

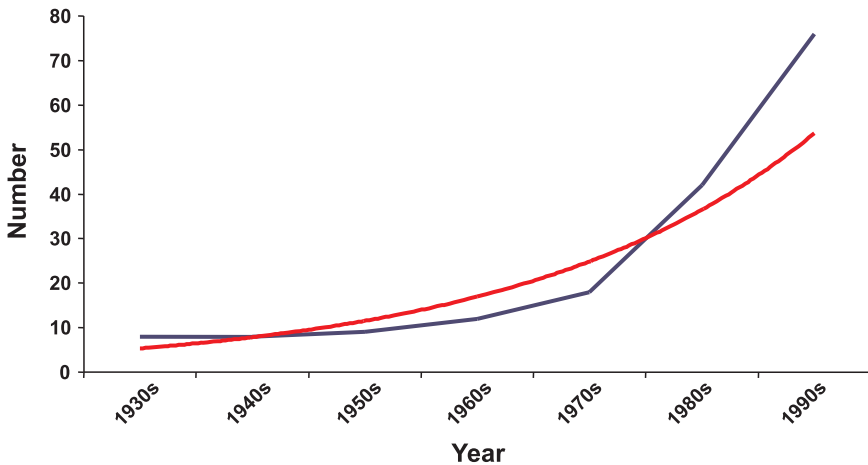


Fig. 2.16 Cumulative growth in reptile and amphibian introductions via the nursery-trade pathway, 1930–1999. Blue line = data for nursery-trade introductions; red line = best-fitting exponential equation for those data, modelled by the function $y = 3.6361e^{0.3844x}$, with $R^2 = 0.8755$

Similarly changeable dynamics characterize the cargo pathway and explain why it has surpassed the “intentional” pathway in numerical importance despite the latter’s considerable and long-standing lead (Fig. 2.15). Visual inspection of the fit of the equation to the cumulative growth curve for the cargo pathway (Fig. 2.17) shows that the equation is being constrained by the simultaneous need to explain relatively low growth rates in the 1850s as well as significantly higher ones later in the 20th century. One can provide a better-fitting model by focusing only those data since the 1890s, the point at which the cargo-pathway data and the exponential model begin to diverge. Doing this (Fig. 2.18) indicates that throughout the 20th century the cargo pathway has actually maintained a higher exponent (0.2943) and, consequently, shorter doubling time (23.4 years) than has the “intentional” pathway

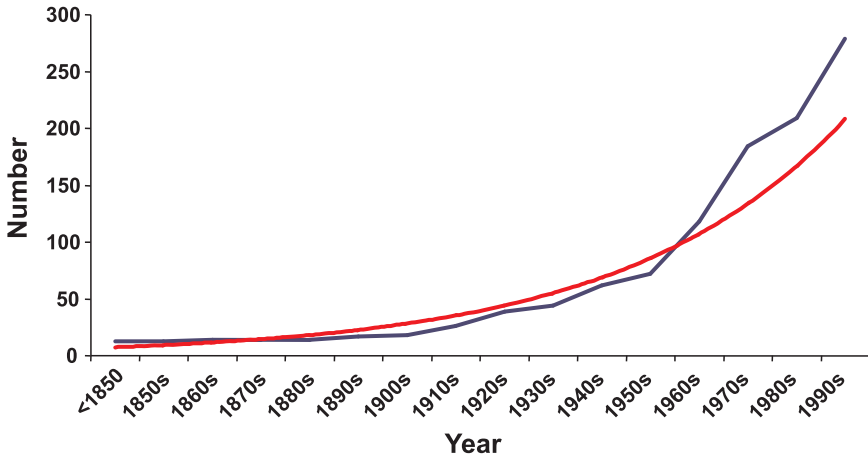


Fig. 2.17 Cumulative growth in reptile and amphibian introductions via the cargo pathway, 1850–1999. Blue line = data for cargo introductions; red line = best-fitting exponential equation for those data, modelled by the function $y = 6.0163e^{0.2215x}$, with $R^2 = 0.9301$

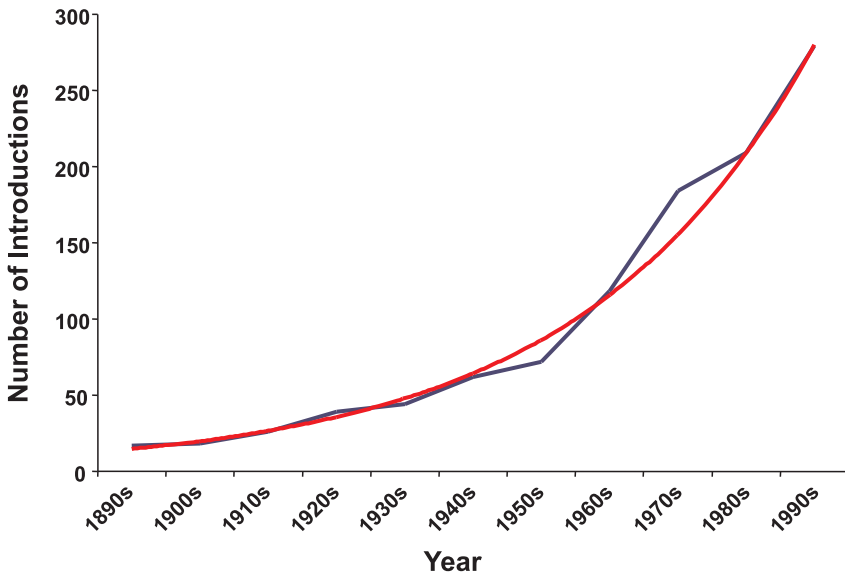


Fig. 2.18 Cumulative growth in reptile and amphibian introductions via the cargo pathway, 1890–1999. Blue line = data for cargo introductions; red line = best-fitting exponential equation for those data, modelled by the function $y = 10.991e^{0.2943x}$, with $R^2 = 0.9888$

(0.1766 and 39.1 years, respectively, for that same period). This accounts for the late 20th century primacy of cargo-mediated over “intentional” introductions.

Another way to more simply summarize recent changes in pathway importance is provided by looking at how the numbers of introductions/year have changed in

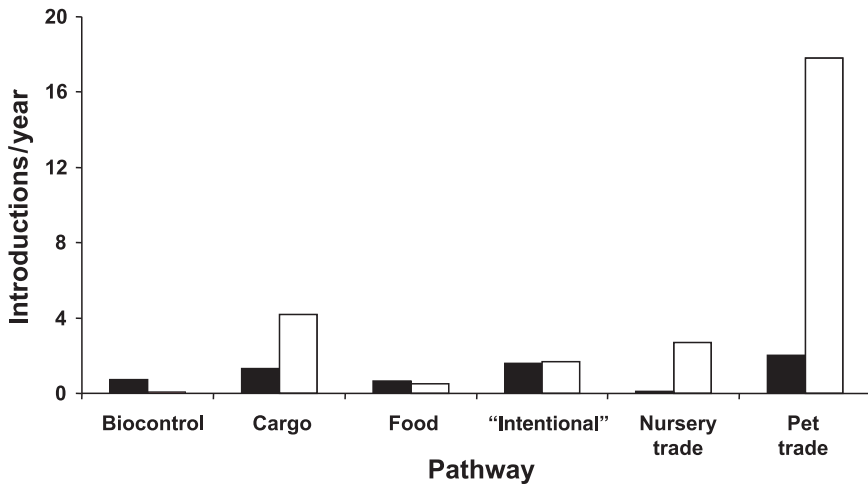


Fig. 2.19 Contrasting introduction rates between the period 1850–1979 (solid bars) vs. 1980–2006 (open bars) for each major introduction pathway

different time periods (Fig. 2.19). It becomes clear at a glance that since 1980, introduction rates for the cargo, nursery, and pet-trade pathways have all been dramatically higher than seen for the prior 120 years, whereas the rate for the bio-control pathway has declined just as dramatically, and the remaining pathways have remained largely the same as their long-term averages. These results are consistent with the variations seen in the exponential models for these pathways, discussed above.

Geographic Variation

Rates of introduction and of successful establishment of alien reptiles and amphibians vary geographically (Fig. 2.20). The large majority of all documented introductions have been to Europe and North America, but successful introductions have been more generally distributed, with the apparent rate of successful introduction varying considerably among recipient regions (Fig. 2.21). This apparent difference is almost certainly a product of two effects, one artifactitious. First, unsuccessful introductions are more likely to be reported in regions having many active scientists and interested naturalists, making rates of successful establishment in such areas appear low compared to regions receiving less scientific attention. And that is the pattern apparent in Fig. 2.21, with the lowest rates of successful establishment obtaining in Europe, North America, and Australia. This is the artifactitious effect reflecting distribution of interested parties to report failed introductions. Second, real regional differences in establishment success probably do occur, independent of the reporting bias. This is most strongly suggested by the three-fold difference in success rate between Europe

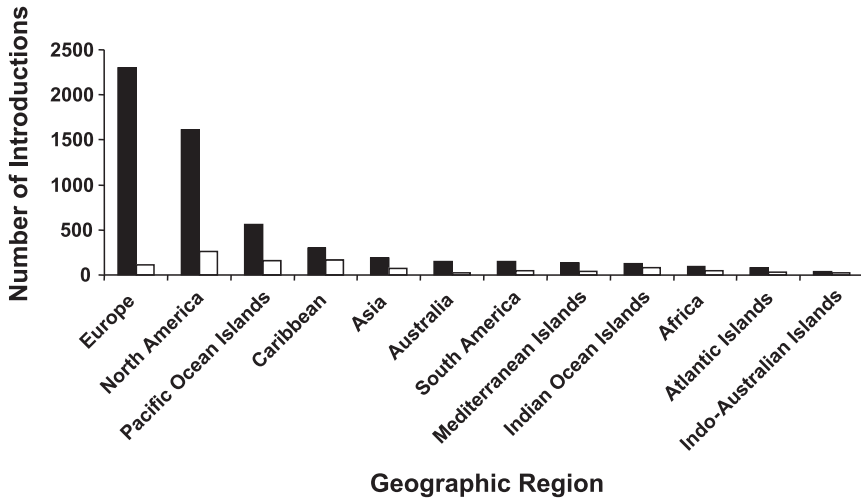


Fig. 2.20 Geographic variation in numbers of reptile and amphibian introductions to recipient regions, measured either as all introductions (solid bars) or only those leading to successfully established populations (open bars). “Europe” excludes the islands of the Mediterranean and Atlantic, which are considered separately

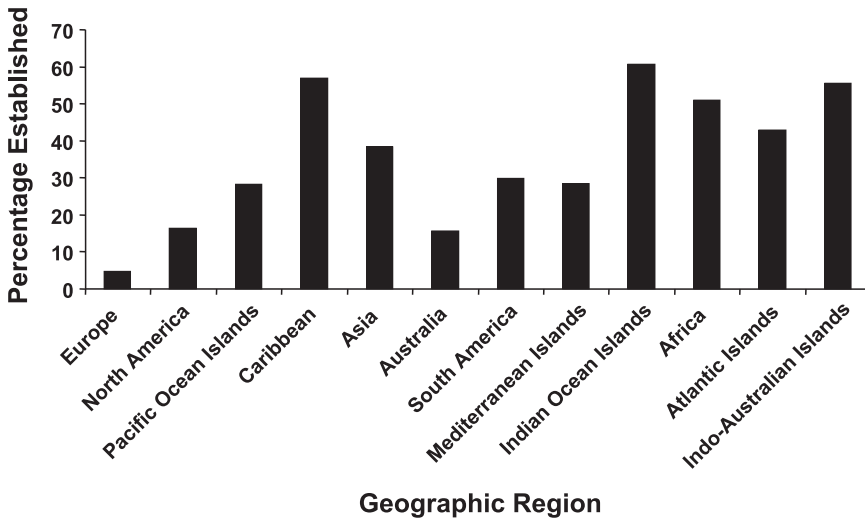


Fig. 2.21 Relative rates of successful population establishment of introduced reptiles and amphibians into each geographic region. “Europe” excludes the islands of the Mediterranean and Atlantic, which are considered separately

and North America, both regions heavily populated with scientists and informed amateurs and both liable to the reporting of anomalous herpetological findings. This difference likely reflects the less hospitable climate of Europe for many introduced reptiles and amphibians, making their chances of successful establishment lower.

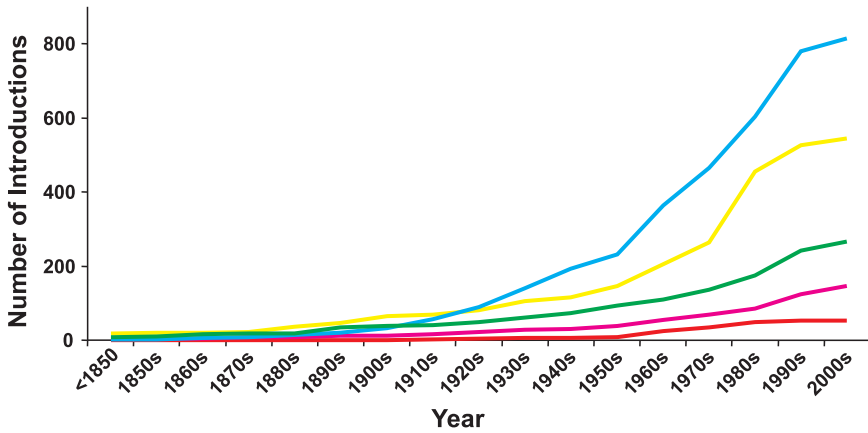


Fig. 2.22 Cumulative growth in reptile and amphibian introductions for the five geographic regions receiving the greatest numbers of introductions. Asia = red, Caribbean = pink, Europe = yellow, North America = blue, and Pacific Islands = green

Table 2.5 Exponential growth rates for regions receiving the greatest numbers of introductions

Pathway	Time span	Growth equation	R ²	Doubling time (years)
Asia	1880–1999	$y = 0.4470e^{0.4114x}$	0.9696	16.8
Caribbean	1850–1999	$y = 3.1657e^{0.2179x}$	0.9875	31.7
Europe	1850–1999	$y = 11.326e^{0.2287x}$	0.9815	30.2
North America	1850–1999	$y = 1.6030e^{0.4133x}$	0.9821	16.7
Pacific	1850–1999	$y = 7.7378e^{0.2089x}$	0.9873	33.0

This same cause is suggested by the higher success rates reported on Mediterranean and Atlantic islands relative to mainland Europe. Both of these insular areas receive adequate or considerable herpetological scrutiny and are unlikely to have unsuccessful establishments heavily under-reported. Differences with mainland Europe likely reflect the more equable climate of the insular areas.

Cumulative growth curves for the five geographic regions receiving the greatest numbers of introductions indicate that each has experienced exponential growth in introduction rates (Fig. 2.22), although Asia has only done so since the 1880s, when the first introductions were documented. Growth rates throughout this 150-year period have been highest for North America, consonant with its high overall numbers of introductions (Fig. 2.20), and for Asia, which trails behind North America in total numbers of introductions (Fig. 2.20) because of its later onset of introductions. Data for Europe suggest a lower growth rate (Table 2.5), but this could partly result from poorer data quality: dates for most European introductions available to me are less well documented in the literature than for North America (dates available for 24% of my European records vs. 51% of those from North America).

Unsurprisingly, pathway importance varies geographically (Figs. 2.23–2.28). Most introductions via the biocontrol and food pathways have been to North America and the Pacific; most cargo introductions have been to these same two areas as well as Australia; most nursery-trade introductions have been to North America and the Caribbean; and most of the “intentional” and pet-trade introductions have been to North America and Europe (Fig. 2.28). For each pathway, two recipient regions dominated introduction volume, together comprising from 48–80% of all introductions within each pathway (Fig. 2.28).

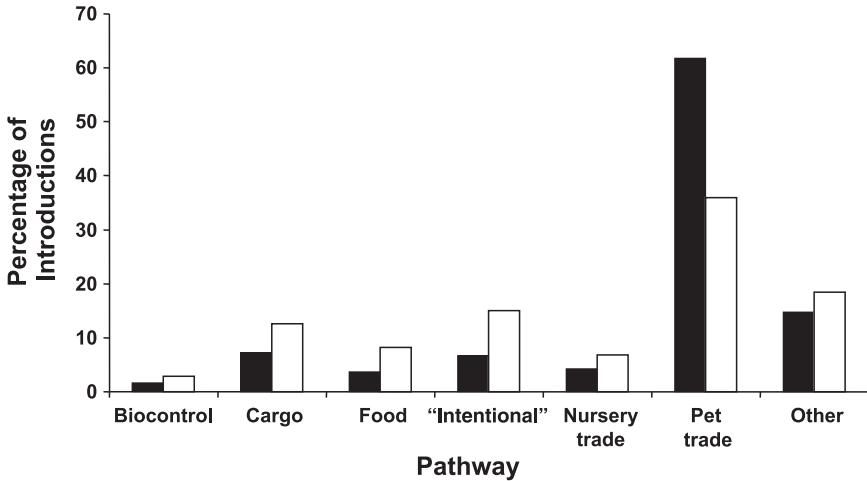


Fig. 2.23 Relative importance of major introduction pathways in North America, as measured by all introductions (solid bars) or only those leading to successful establishment (open bars)

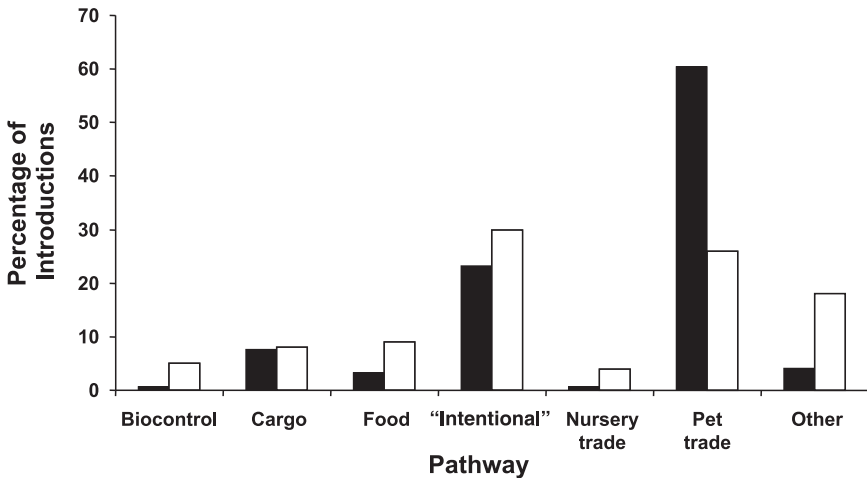


Fig. 2.24 Relative importance of major introduction pathways in Europe, as measured by all introductions (solid bars) or only those leading to successful establishment (open bars)

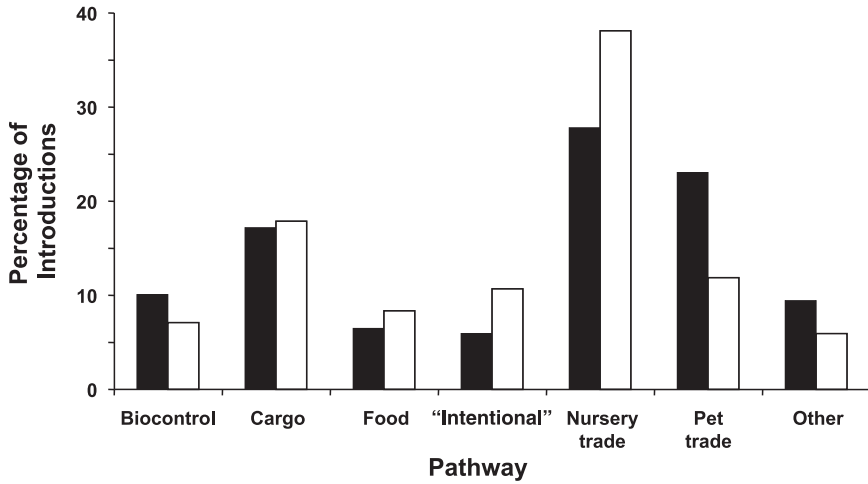


Fig. 2.25 Relative importance of major introduction pathways in the Caribbean, as measured by all introductions (solid bars) or only those leading to successful establishment (open bars)

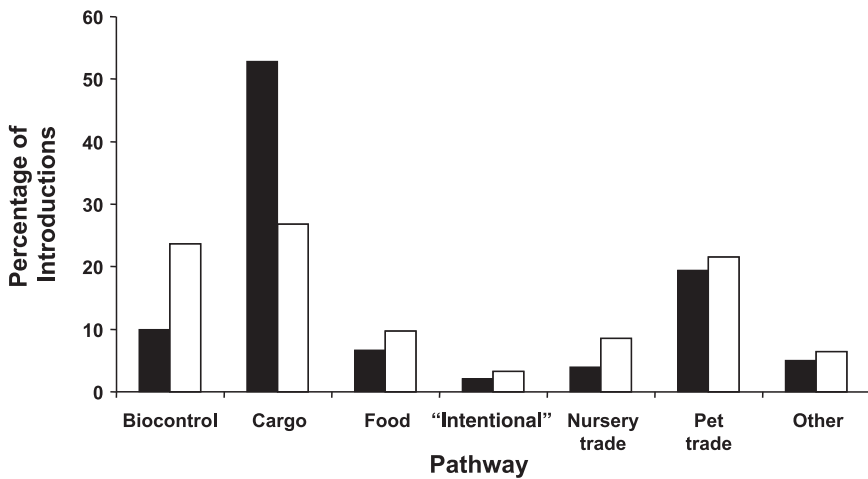


Fig. 2.26 Relative importance of major introduction pathways in the Pacific Islands, as measured by all introductions (solid bars) or only those leading to successful establishment (open bars)

Within the 12 regions examined, eight have received introductions representative of all six major pathways, two have five pathways represented, and only two have as few as four pathways (Fig. 2.29). For most regions, introductions are dominated by only one or two pathways, but pathway importance varies between regions. Single pathways accounting for >50% of all introductions within a recipient region include the pet trade in Europe, North America, the Atlantic Islands, South America, and Asia, and cargo in Australia and the Pacific Islands (Fig. 2.29).

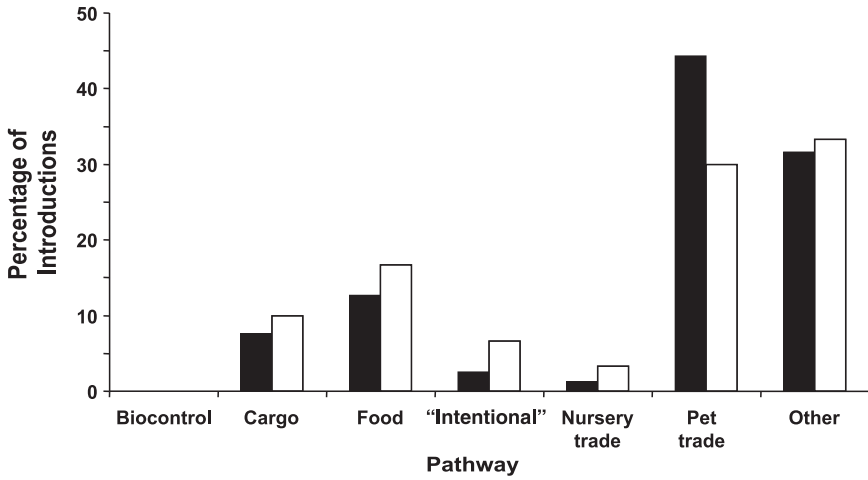


Fig. 2.27 Relative importance of major introduction pathways in Asia, as measured by all introductions (solid bars) or only those leading to successful establishment (open bars)

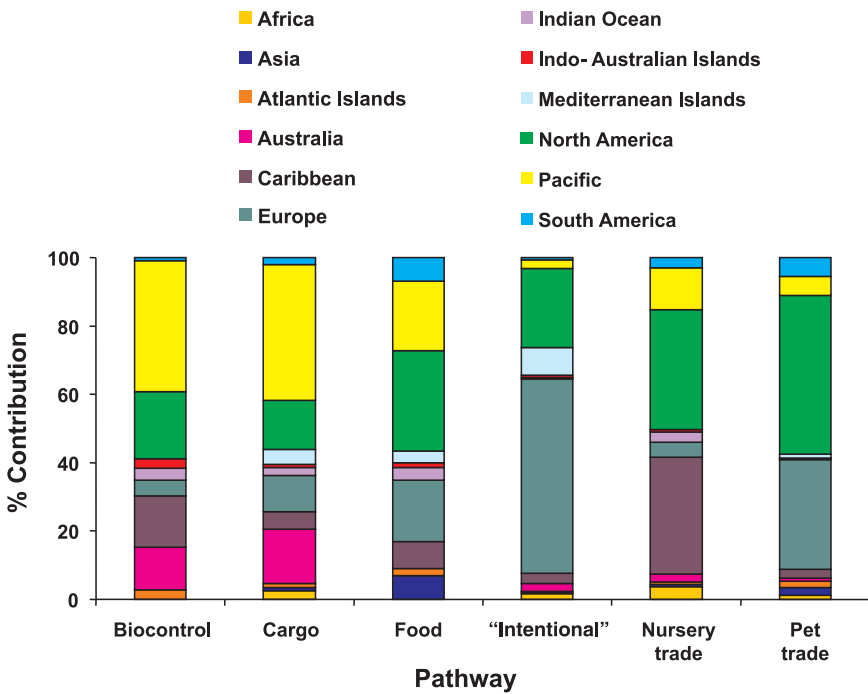


Fig. 2.28 Relative dominance of each recipient region for each major introduction pathway

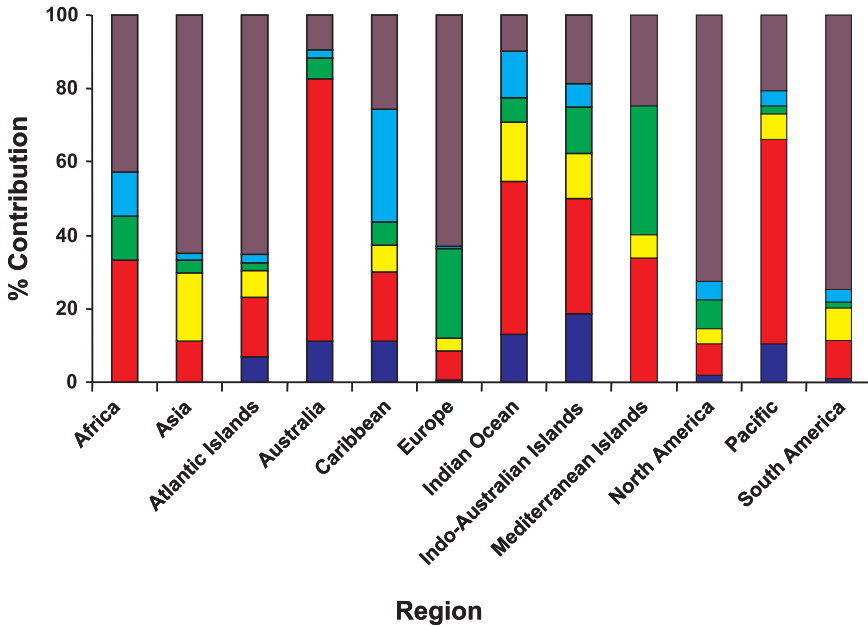


Fig. 2.29 Relative pathway importance for each recipient region. Biocontrol = dark blue, cargo = red, food = yellow, “intentional” = green, nursery trade = blue, and pet trade = brown

Other regions have a less-skewed distribution of pathways, but most are still dominated by two (Fig. 2.29). Some introduction pathways were not represented in particular regions. For example, biocontrol introductions are lacking for Africa, Asia, and the Mediterranean Islands; introductions for food are unreported for Africa and Australia; and the nursery pathway is unrepresented among introductions to the Mediterranean Islands (Fig. 2.29).

One may also contrast success rate and pathway importance not by geographical region but by type of landform, in particular contrasting patterns between islands vs. continents. If one contrasts rate of successful establishment onto islands vs. continents, one finds the rate considerably higher in the former than the latter (35% vs. 12%), a difference that is statistically significant ($G = 279.468$, $DF = 1$, $p = 4.90e^{-63}$). This difference is mostly due to higher establishment success rate on small islands. If one contrasts small islands (<6,000 km²), large islands (>8,000 km²), and continents with each other, one finds the rate of successful establishment on small islands to be more than twice that on large islands and approximately four times that on continents (Fig. 2.30), a difference that is again statistically significant ($G = 388.377$, $DF = 2$, $p = 4.62e^{-85}$). Conversely, if one contrasts large islands with continents (Fig. 2.30), a difference remains between the two but is of much less magnitude ($G = 14.37$, $DF = 1$, $p = 0.00015$). Islands thus appear more susceptible to successful establishment of alien populations than do continental areas, and islands smaller than the size of Puerto Rico are especially so.

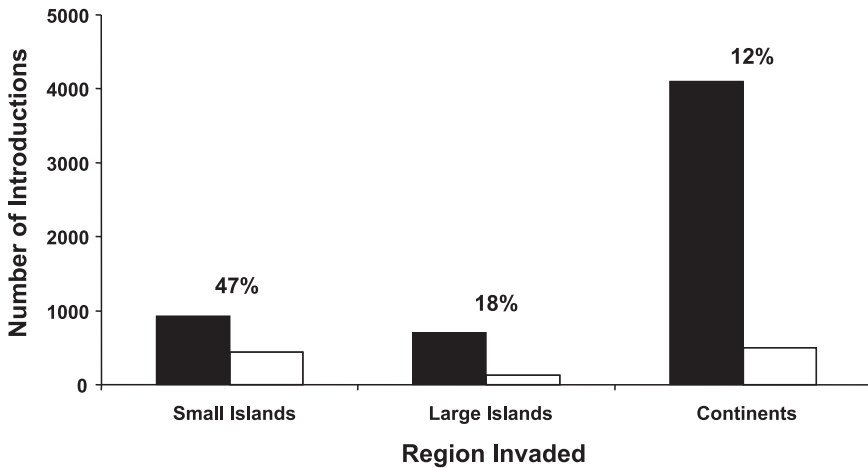


Fig. 2.30 Distribution of the numbers of introductions among small islands, large islands, and continents. Bars are the total sum of introductions (solid bars) and sum of introductions leading to successful establishment (open bars), with establishment counted only once per jurisdiction. Numerical values are percentages of introductions resulting in successful establishment of populations. Differences in establishment rate are highly significant ($G = 388.377$, $DF = 2$, $p = 4.62e^{-85}$)

Relative pathway importance also varies among these three categories of recipient landmasses. Introductions to continents have been dominated by the pet-trade pathway, and those to large islands by the cargo pathway (Fig. 2.31). In contrast, those to small islands have involved a more even distribution of pathways, with cargo and pet-trade pathways predominating, but with biocontrol, food, and nursery trade pathways exhibiting greater importance than seen for continents (Fig. 2.31). Some of these differences are less obvious if one considers only successful introductions. In that case, the pet-trade pathway is still of predominant importance for continental situations, but successful introductions to both large and small islands have resulted from a more even distribution of pathways (Fig. 2.32). In this case, the cargo pathway still leads to the largest number of successful introductions on small islands, but both the cargo and “intentional” pathways have resulted in the highest numbers of established populations on large islands.

The largest number of introductions have involved species originating from North America, with lesser numbers originating from Asia, Europe, and Africa (Fig. 2.33). However, if the immensely popular *Trachemys scripta* is excluded from these numbers, the predominance of North America declines to a value of 1,330, only somewhat greater than that for Asia. As seen earlier, successful introductions are less frequent (Fig. 2.33). In this respect, species originating from insular regions appear to have resulted in more establishments than those from continental regions (Fig. 2.34). This pattern could result for different reasons. First, it may be an artifact that these insular species have most often been moved to other islands whose habitats are similar enough to promote a high probability of establishment.

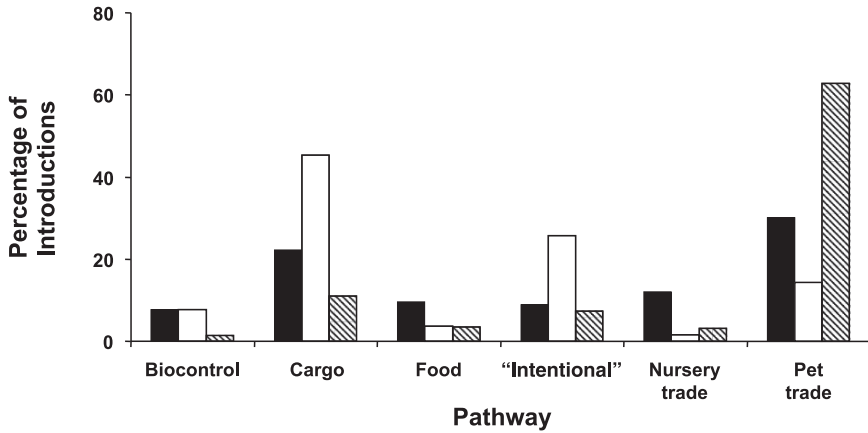


Fig. 2.31 Variation in relative pathway importance among small islands (solid bars), large islands (open bars), and continents (diagonally hatched bars) across all introductions

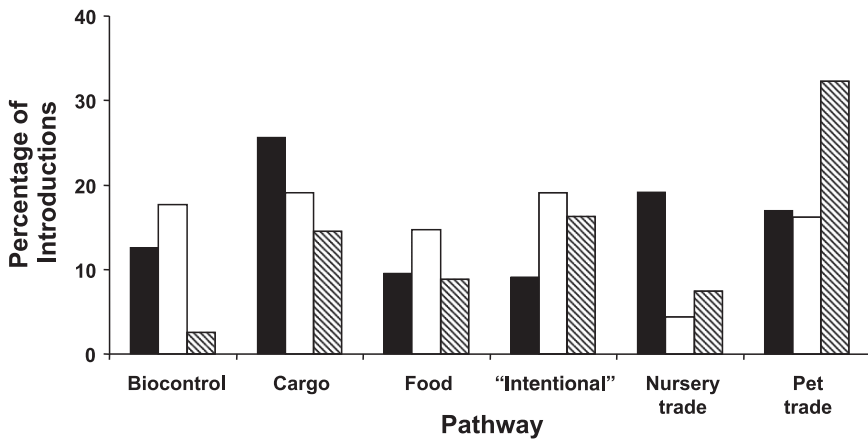


Fig. 2.32 Variation in relative pathway importance among small islands (solid bars), large islands (open bars), and continents (diagonally hatched bars) only for those species having successfully established populations

Alternatively, species from continents may more often be introduced to a wider variety of habitats, thereby decreasing their probability of successful colonization. Second, it may be that species native to insular regions are ecologically and physiologically preadapted for successful colonization, giving them a relative edge over species from continental areas. These hypotheses are not mutually exclusive.

Lastly, growth in importance of the major source areas for introduced species is similar to that seen in earlier figures, although it is not so consistently exponential as seen for the other cumulative growth patterns (Fig. 2.35). Such exponential

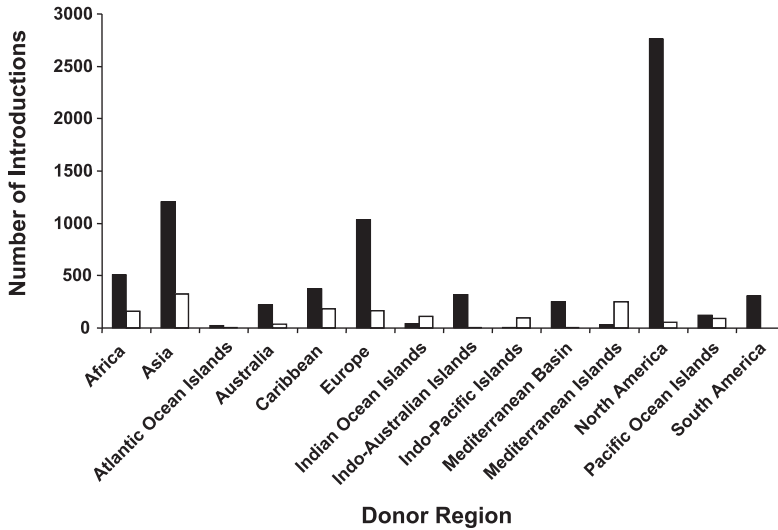


Fig. 2.33 Relative contributions of each donor region to global introductions of reptiles and amphibians, as measured by all introductions (solid bars) or only those leading to successful establishment (open bars). Note that geographic regions are not necessarily mutually exclusive because species’ native ranges may include more than one region and because species occurring in the Mediterranean region were parsed into different, non-exclusive categories (“Europe”, “Mediterranean Basin”, “Mediterranean Islands”)

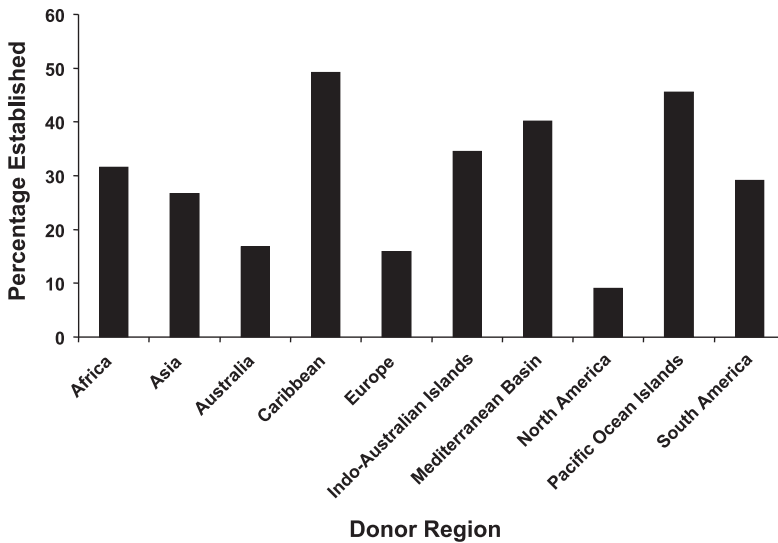


Fig. 2.34 Relative rates of successful population establishment of introduced reptiles and amphibians derived from each donor region, restricted to only those regions donating more than 100 introductions. Categorical caveats as for Fig. 2.33

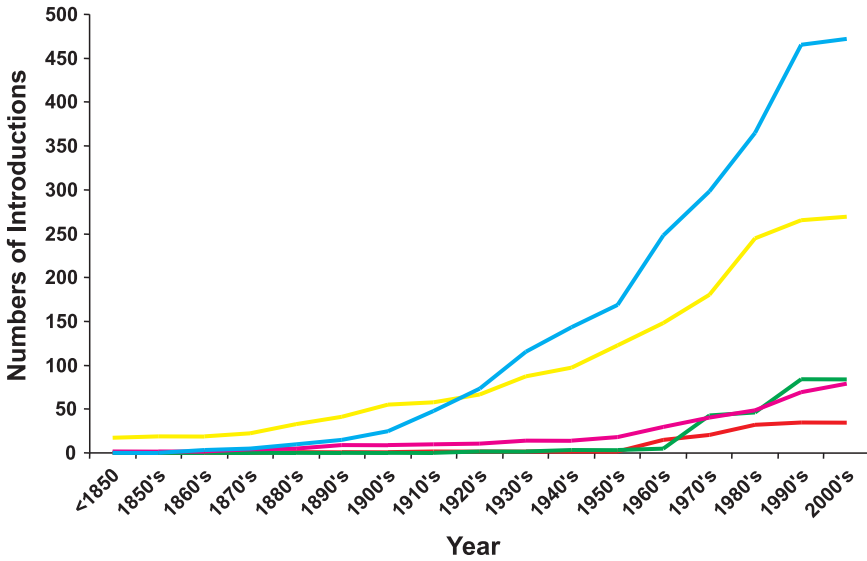


Fig. 2.35 Cumulative growth in donor region contribution to global reptile and amphibian introductions. Asia = red, Australia = green, Caribbean = pink, Europe = yellow, and North America = blue

Table 2.6 Exponential growth rates for regions donating the greatest numbers of introductions

Pathway	Time span	Growth equation	R ²	Doubling time (years)
Caribbean	1850–1999	$y = 1.4440e^{0.2329x}$	0.9683	29.6
Europe	1850–1999	$y = 12.295e^{0.1932x}$	0.9909	35.7
North America	1900–1999	$y = 26.573e^{0.3031x}$	0.9633	22.8

growth as does occur (Table 2.6) is consistent with the hierarchy in dominance of donor regions seen in Fig. 2.35. The greater variation in growth patterns seen for donor regions compared to the strictly exponential patterns seen earlier for recipient regions (Fig. 2.22, Table 2.5) likely reflects the importance that legal and aesthetic particularities can have in restricting what is available for transport from a single region at any particular time. In contrast, importations to a region can average across a diversity of source areas, smoothing out availability variation in source areas, and thereby keeping growth at a more consistently exponential rate.

General

Although I have identified a total of ten pathways by which alien herpetofauna are transported, and six major pathways that account for most of this transport, several of these are clearly related to each other. For example, two of the major

pathways – the pet trade and “intentional” pathways – are intimately related and form a nexus of aesthetic motivation. Included in this too are the minor pathways of exhibit and zoo releases. These four pathways combine to form the primary means by which alien herpetofauna have been moved and naturalized in the past several decades (Fig. 2.36). They clearly represent a deliberate failure of social responsibility among the citizenry of many countries. The major pathways of cargo stowaways and nursery trade – as well as the minor pathways of aquaculture contamination and vehicle stowaways – also represent a single general nexus representing unintentional transport as a direct consequence of increasing international trade volume. These do not constitute a failure of personal responsibility so much as a failure to recognize a statistically predictable phenomenon and programmatically respond to it. This is the second major axis of modern introductions (Fig. 2.36). Between these axes of aesthetic motivation and contaminated trade goods the majority of modern herpetofaunal introductions are accounted for. The deliberate pathways involving introduction for biocontrol or for food use have become minor in the second half of the 20th century (Fig. 2.15), although the latter is still an important means of introducing the problematic bullfrog (*Rana catesbeiana*) to many developing counties. Given the ecological impacts that this species likely inflicts (see following chapter), its introduction alone merits the effort to close the food pathway, even though overall magnitude of that pathway is now small.

Despite the fact that the generalizations discussed here have been focused on major introduction pathways, it must be borne in mind that the minor pathways cannot be

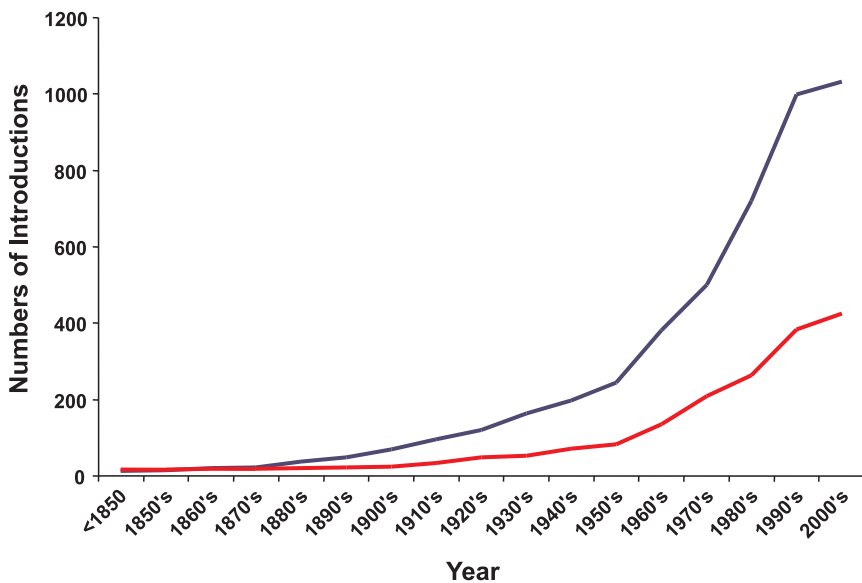


Fig. 2.36 Cumulative growth in importance of deliberate aesthetic motivations leading to herpetological introductions (blue) vs. unintentional introductions resulting from trade activities (red)

discounted or altogether ignored. And “minor” pathways can actually form a significant percentage of all introductions for some taxonomic groups. Although the contribution of minor pathways to the total introduction volume of heavily transported taxa is typically small (e.g., 6.3% for lizards, 3.2% for snakes, and 2.3% for turtles), they account for an important component of total volume for frogs (13.1%) and crocodylians (18.8%), and they actually account for the majority (59.5%) of salamander introductions. But that last observation is somewhat anomalous, with 38.8% of all salamander introductions resulting from deliberate introductions for scientific research, and 83% of these done by one individual in a “research” program of doubtful scientific relevance. If these 39 introductions are excluded, the percentage of salamander introductions due to “minor” pathways is reduced to 40%. This is still a much larger number than seen for other taxa, and it reflects the importance of bait use and the residual research introductions in accounting for salamander dispersal by humans.

A related caveat applies to the taxonomic analyses. Even though I have demonstrated which taxa predominate in herpetofaunal introductions (Figs. 2.2–2.5), it is important to remember that not all taxa pose equal ecological or economic hazard. So some species or higher taxa may be capable of generating damage disproportionate to their contribution to overall introduction volume. As just one example of particular concern, snakes only rate as the fourth-most-frequently introduced taxon of alien reptiles and amphibians (Fig. 2.3), comprising 11% of all herpetofaunal introductions. Yet dangerously venomous or powerful snakes make up a disconcertingly large portion (20%) of that total, a fact that increases the concern that might be accorded that segment of herpetofaunal introductions. Successful naturalization of such species has already occurred in Okinawa and Florida, and serious impacts are anticipated to follow (see next chapter).

My prior analysis of an early subset of the current database (Kraus, 2003c) concluded that the rate of successful establishment among introduced reptiles and amphibians was much higher than expected from the so-called “tens rule”. This rule postulates that approximately 10% of alien species imported to an area appear in the wild (are “introduced”, as I have been using the term), 10% of introduced species become naturalized, and 10% of naturalized species become invasive (Williamson and Brown, 1986; Williamson and Fitter, 1996). Since the rule is statistical, the probability of successful transition from imported to introduced, introduced to established, and established to invasive can vary from roughly 5–20% at each stage and still be viewed as according with the rule (Williamson, 1996). I have no data to address the first transition (from importation to introduction) because I have not gathered data on contained importations, such as those for the pet trade, nor for the third transition (from establishment to invasiveness) because most naturalized reptiles and amphibians have not been investigated for invasiveness. Data presented here (Fig. 2.5), however, make clear that the transition from introduction to establishment is higher for some taxa than predicted by the tens rule. In particular, frogs and lizards appear to have been more successful at naturalizing than predicted. And even salamanders and snakes lie on the high end of the range acceptably compliant with the tens rule. The same conclusion attended my earlier analysis, but the present conclusion is more compelling because the denominators now include information on multiple introductions

per jurisdiction. However, the values in Fig. 2.5 will be slight underestimates because multiple naturalizations within a single jurisdiction will not appear in the numerators. Failure of the tens rule has been found across a variety of other taxa as well (Hayes and Barry, 2007), so its success as a rule may be uncertain

What implications do the data and patterns discussed herein have for responding to herpetofaunal invasions? I would suggest that the scope of data employed in the above analyses is sufficiently comprehensive that additional study to gain a clearer picture of global patterns of this phenomenon is not required, although, no doubt, improvements could be made in understanding the dynamics of introduction within particular jurisdictions by the application of data not used herein, such as information on importation volume and species composition. What is abundantly clear from the preceding analyses is that herpetological introductions are growing exponentially in most regions of the world and that they involve all major taxa and a diversity of pathways. This is not a phenomenon limited to iconically invaded locations like Florida or Hawaii. Unlike many other major taxa (e.g., plants, birds, marine invertebrates), whose transport is dominated by one or a few intentional or accidental pathways, herpetofaunal introductions involve a mix of both. So, unlike many other taxa, successfully managing herpetofaunal introductions must involve responding to both. Despite this, I have clearly demonstrated that the pet-trade and aesthetically related pathways – pathways that promote the keeping of animals and their frequent escape, release, or intentional introduction via private owners, wholesalers, retailers, exhibitors, or zoo personnel – are of overwhelming importance in creating the modern explosion of alien herpetofaunal invasions. The growing cargo and nursery-trade pathways cannot safely be ignored, but if herpetofaunal invasions are to be stopped, it must be a first priority to halt the careless or arrogant release of animals by pet fanciers, dealers, and zoo personnel. The means of doing this, and further implications of these pathway-analysis findings for management and research, will be considered in detail in the final chapter, which is devoted to that subject.

Chapter 3

Impacts of Alien Reptiles and Amphibians

The entire motivation for concerning ourselves with invasive alien species, of course, relates to the ecological and economic damage these species cause. For many non-herpetological taxa, as noted in Chapter 1, damages have been extensive and severe, justifying the considerable attention that has been devoted to a host of invasive pests of all groups. As for these better-known taxa, when determining the degree of attention that alien reptiles and amphibians might merit as a management problem it is imperative to assess to what extent these species inflict damage. Clearly, if these animals are not affecting natural or human ecosystems, concern for their introduction will be lessened. And, indeed, it has been argued that most reptile and amphibian introductions to Florida provide no such impact, and the threat of alien herpetofauna there has been largely discounted (L.D. Wilson and Porras, 1983; Butterfield et al., 1997). Alternatively, if it be shown that alien reptiles and amphibians do cause an array of ecological or societal damages, a greater responsibility for management response would inhere. In either event, a broader awareness of these impacts or their absence would improve our assessment of the relative standing of alien reptiles and amphibians as environmental, conservation, or social problems. It would concomitantly serve to identify obvious research needs for further clarifying extent and ecological mechanisms of impact as well as control and mitigation measures.

A broad survey of ecological impacts attending invasive reptile and amphibian introductions has not previously been available. In providing one here, I confine my attention to studies that clearly demonstrate some level of impact from alien herpetofauna and that provide some evidence or compelling argument as to what the mechanism of such impact might be. In including instances that provide only reasoned argument to identify impact mechanism I hope to highlight several hypotheses that have languished in the literature for lack of further investigation. The literature occasionally contains correlational evidence that simply notes the decline or disappearance of a native species to be coincidental with expansion of a naturalized alien (e.g., Münch, 2001). However, such correlations need not result from the introduced alien per se; both species may simply be responding differently to underlying environmental changes (cf. L.D. Wilson and Porras, 1983 for herpetological examples). Such instances are generally omitted in this summary because evidence identifying the causative mechanism of replacement is not provided.

Nonetheless, such correlational evidence points to additional potential instances of detrimental impacts that may warrant investigation. Lastly, concerns have frequently been expressed in the literature for a variety of potential impacts for which no evidence is provided whatsoever. Some of these speculations may be valid, but in the absence of documentary evidence or reasoned argument they do not approach minimal scientific standards and are ignored here.

This survey reveals that a surprisingly wide array of deleterious impacts are documented across a variety of herpetological species, even though taxonomic sampling among naturalized herpetofauna has been sparse. Indeed, research into impacts from alien reptiles and amphibians is rather recent, and it is to be expected that additional examples and further impacts will be identified as research into this area garners greater momentum. Impacts identified to date may be broadly categorized as ecological, evolutionary, or social. The first includes impacts on individual species as well as broader community-level disruptions. Ecological damages from alien herpetofauna most often derive from food-web disruptions, with impacts stemming from predation on sensitive species, poisoning of predators, competition with natives, vectoring of novel parasites, or secondary disruption of food webs. Evolutionary impacts encompass genetic contamination via hybridization with natives as well as changes in inherited morphological, physiological, or behavioral traits. Genetic impacts relate to introgression of alien genes into native gene pools, sometimes to the point of genetically swamping native forms out of existence. Under the category of evolutionary change are included both changes observed in the invasive alien as well as modifications induced in native fauna by its introduction. Social damages include direct impacts on humans or their cultural institutions. These impacts can be to human health, economies, quality of life, or scientific knowledge.

Ecological Effects

Removal of Native Prey Species

The most widely studied and commonly considered ecological effect from alien reptiles and amphibians is predation on sensitive native species resulting from the introduction of novel predators. In only a few instances has direct evidence of population-level effects on natives been demonstrated, but many anecdotal observations suggest it may be a frequent phenomenon. This is, however, difficult to document because intense, novel predation may provide only a narrow window of opportunity for observing populations during the phase of decline. More often, sudden rarity is noticed after the fact and the cause can only be inferred retrospectively by temporal correlation with a newly introduced predator.

The best-known instance of predation leading to loss of native species is the introduction of the brown treesnake (*Boiga irregularis*) to Guam in the years

immediately following World War II. This snake caused the loss from Guam of ten forest bird, three seabird, 1–3 bat, and six lizard species within a span of approximately 40 years (Savidge, 1987a; Engbring and Fritts, 1988; McCoid, 1991; Rodda and Fritts, 1992; Fritts and Rodda, 1995, 1998; Rodda et al., 1997, 1999b; Rodda and Savidge, 2007). Three of the birds and one bat were endemic to Guam and are, therefore, globally extinct. Two further bird species remain only in captivity, and most of the native vertebrates remaining on Guam do so at extremely reduced abundances (Rodda and Savidge, 2007), where too they may be susceptible to predation by other introduced reptiles, such as *Varanus indicus* (McCoid and Hensley, 1993a). This introduced snake population has been the subject of scores of studies, and early ecological research clearly ruled out a variety of other hypotheses to explain the observed bird declines (Savidge, 1987a; Savidge et al., 1992). The dire effects caused by this snake have led to a 14-year control program to prevent the species colonizing additional Pacific islands, but indications are that Saipan may now be invaded as well. If true, similar ecological effects may be expected there in the coming decades (Fritts and Rodda, 1995; Rodda et al., 1999b).

The snake *Natrix maura* was introduced to the Balearic Islands approximately 2,000 years ago (Alcover and Mayol, 1981). It is credited with reducing the range of the formerly island-wide endemic frog *Alytes muletensis* to plunge pools in a few steep-sided gorges in the uplands of Mallorca (Tonge, 1986; Moore et al., 2004a; Pleguezuelos, 2004). It is also thought to have played a role in the extinction of the endemic *Alytes talaioticus* during the Holocene (Pleguezuelos, 2004). Evidence for these claims lies in the highly ravenous behavior of *N. maura*, its absence from fossils predating human settlement of the islands, and the persistence of *A. muletensis* at elevations where the snakes are scarce (Alcover and Mayol, 1981; Tonge, 1986; Moore et al., 2004a).

The lizard *Anolis carolinensis* was introduced to Chichijima in the Ogasawara (Bonin) Islands in the period from 1965–1968 (M. Hasegawa et al., 1988) and subsequently released on Hahajima in 1981 (Miyashita, 1991). It has expanded its range quickly (M. Hasegawa et al., 1988) and increased to tremendous population densities ranging from 600–2,570 animals/ha and averaging 1,270 animals/ha (Okochi et al., 2006). Feeding trials, direct observations, and stomach-content analyses have demonstrated this lizard to feed on a variety of native insects (Karube, 2004b, 2006; Karube and Suda, 2004; Makihara et al., 2004). Comparisons of insect faunas on Chichijima and Hahajima before and after *Anolis* invasion, as well as comparisons between these islands and nearby uninvaded islands, correlate the decline or extirpation of several formerly common species of buprestid, cerambycid, cucurionid, and melandryid beetles; lycaenid and papilionid butterflies; bees; and odonates to that invasion (Karube, 2004a, b, 2005; Karube and Suda, 2004; Makihara et al., 2004; Takakuwa and Suda, 2004; Yoshimura and Okochi, 2005; Okochi, et al., 2006). To date, toxic, nocturnal, and large, hard-bodied species have not experienced catastrophic declines (Makihara et al., 2004; Karube, 2005). In all, at least 15 species of endemic insects appear to have vanished or strongly declined because of the lizard. Most of these are small, diurnal, non-toxic species with a fondness for resting on the sunlit vegetation favored by the lizards

(Karube, 2001, 2004a; Karube and Suda, 2004). Although preferred prey are small diurnal inhabitants of vegetation, *A. carolinensis* has also been documented foraging on large, hard-bodied cicadas, strictly ground-dwelling species, and nocturnal species sleeping in leaf axils, with the last apparently leading to declines in some nocturnal cerambycids as well (Karube and Suda, 2004; Karube, 2005). This switch from preferred prey is thought to result from declining resources (Karube and Suda, 2004; Karube, 2006), and it is anticipated that yet additional insects will disappear from Hahajima and Chichijima as more preferred prey species disappear (Karube and Suda, 2004). Persistence of some of these endangered insects on adjacent islands may be only temporary inasmuch as poor-quality habitat makes them population sinks that historically were replenished by migration from the two islands now having *Anolis* infestations (Takakuwa and Suda, 2004).

The related *Anolis sagrei* was introduced to Florida in the mid- to late-1800s (Garman, 1887; W. King and Krakauer, 1966) and has rapidly expanded across the state (Campbell, 2003a). During this expansion it has frequently been noted that the native *A. carolinensis* has either disappeared or declined in numbers in many populations (Tokarz and Beck, 1987; P.R. Brown and Echternacht, 1991; Echternacht, 1999), and rapid replacement of that native by *A. sagrei* has been experimentally demonstrated in the field (T. Campbell, 1999a). In highly disturbed habitats, it appears that *A. carolinensis* can disappear entirely, but in more structurally complex habitats it persists at lower population densities occasioned by its occupancy of fewer, elevated territories than prior to invasion by *A. sagrei* (Echternacht, 1999). Decline of the native appears largely due to predation on *A. carolinensis* hatchlings by *A. sagrei*, with preference shown by *A. sagrei* for consumption of heterospecific hatchlings over conspecific hatchlings in the laboratory (Gerber, 1991; Gerber and Echternacht, 2000), and predation on hatchlings on *A. carolinensis* documented in the field (T. Campbell and Gerber, 1996). Hatchlings of both species live near ground level, thus bringing them in frequent contact with dense populations of adult *A. sagrei* (but not *A. carolinensis*) and making them susceptible to predation by that species (Echternacht, 1999). The dense populations routinely formed by *A. sagrei* place the hatchlings of the sparser *A. carolinensis* in peril wherever insufficient ground cover is available for refugia (T. Campbell, 1999a), and occasional consumption of an *A. carolinensis* hatchling is all that is needed to severely depress recruitment in that species (Echternacht, 1999). This appears to explain the observed inability of *A. carolinensis* to persist in sympatry with *A. sagrei* in heavily modified habitats lacking structural diversity.

The rapid spread of introduced *Anolis sagrei* and observed shift in perch heights of native *A. conspersus* in the Cayman Islands (Losos et al., 1993) are likely accounted for by similar dynamics. In that case too, laboratory trials have indicated an asymmetrical preference of adult *A. sagrei* for consuming *A. conspersus* hatchlings (Gerber and Echternacht, 2000). This, combined with the dense populations again seen in *A. sagrei* and the occupation by hatchling *A. conspersus* of lower vegetational strata, would provide a similar mechanism for population declines in the native anole (Gerber and Echternacht, 2000) as seen for Floridian *A. carolinensis*.

Cane toads (*Bufo marinus*) introduced to Australia have been documented to inflict population-level effects on the ground-nesting rainbow bee-eater (*Merops ornatus*). In the absence of toads, these birds produce an average of 1.2 fledglings/nest. But toads prey upon eggs and nestlings and usurp nest burrows, thereby destroying one-third of all nests and reducing nest success rate to an average of 0.8 fledglings/nest (Boland, 2004a, b). Displaced adult birds suffer reduced average nest productivity with subsequent nesting attempts, making the effects of the toads even broader than that measurable by direct predation and nest destruction (Boland, 2004a, b). Susceptibility to nest predation by toads appears to result at least partly from lack of proper defensive behaviors in the nesting birds, which can successfully fend off attacks by much larger native predators (Boland, 2004a, b). Cane toads have been reported to prey on an array of other native vertebrates (e.g., Rabor, 1952; Pippet, 1975; Stammer, 1981; Freeland and Kerin, 1988; Caudell et al., 2000), but effects on populations have not been systematically researched. One study reported a correlation between presence of toads and reduction in beetle populations (Catling et al., 1999); another reported a similar correlation with a reduction in gecko populations (Watson and Woinarski, 2003, cited in McRae et al., 2005). Others have noted toads to have greater volumes of prey in their stomachs where recently established compared to areas where they have been longer established (Anonymous, 1968), suggesting suppressive effects on invertebrate communities by a prolonged history of predation, although temporal changes in invertebrate populations have not been measured directly. Anecdotal reports of pest and native invertebrate declines following introduction of toads (e.g., Wolcott, 1937, 1948, 1950a, b; Simmonds, 1957) suggest the same suppressive effects, but studies on most native invertebrate communities are lacking (but see Greenlees et al., 2006 for an exception).

A variety of studies has implicated alien bullfrogs (*Rana catesbeiana*) in declines of native herpetofauna across the western United States. Evidence includes anecdotal (Lardie, 1963; Dumas, 1966; Hammerson, 1982) and statistical (Moyle, 1973; Schwalbe and Rosen, 1988; Fisher and Shaffer, 1996; Kupferberg, 1997a; Rosen and Schwalbe, 2002) analyses of distributional or historical trends, partial recovery of affected populations with experimental reduction or enclosure of bullfrogs (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1996a, b), skewed size-class distributions in populations syntopic with bullfrogs (Holland, 1991, cited in Hayes et al., 1999), and experimental demonstration of increased mortality or decreased growth in laboratory or field experiments (Kiesecker and Blaustein, 1997, 1998; Kupferberg, 1997a; Lawler et al., 1999; Adams, 2000; Pearl et al., 2004; Maret et al., 2006). Natives argued to be affected by bullfrogs include the frogs *Bufo boreas* (Lardie, 1963), *Pseudacris regilla* (Jameson, 1956), *Rana aurora* (Lardie, 1963; Pearl et al., 2004), *R. blairi* (Hammerson, 1982), *R. boylei* (Moyle, 1973; Kupferberg, 1997a), *R. chiricahuensis* (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1995, 2002; Rosen et al., 1995), *R. draytonii* (Moyle, 1973); *R. pipiens* (Hammerson, 1982), *R. pretiosa* (Lardie, 1963; Dumas, 1966; Pearl et al., 2004), *R. yavapaiensis* (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1995, 2002), the entire suite of central Californian amphibians (Fisher and Shaffer, 1996), the

turtle *Actinemys marmorata* (Hays et al., 1999), and the snake *Thamnophis eques* (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1995, 2002). Similar declines in native herpetofauna concurrent with introduction of bullfrogs have been noted in Germany (C.R. Boettger, 1941; Thiesmeier et al., 1994). Because of the bullfrog's catholic, opportunistic diet (Bury and Whelan, 1984) and numerous observations of predation on sensitive species (Table 3.1), declines have most often been attributed to bullfrog predation. This interpretation is bolstered by scarring and tail loss seen on affected natives and by skewed population structures consistent with predation on juveniles (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1995). Furthermore, experiments have confirmed bullfrogs to mediate their negative effects in part via direct predation (Kiesecker and Blaustein, 1997). However, bullfrogs can also induce behavioral changes in microhabitat use by natives that decrease the latter's survival and growth rates (Kiesecker and Blaustein, 1998). Further, a variety of other factors, including habitat modification or loss (Moyle, 1973; Hayes and Jennings, 1986; Jennings, 1988b; Fisher and Shaffer, 1996; Adams, 1999, 2000; Kiesecker et al., 2001; Davidson et al., 2002; Rosen and Schwalbe, 2002), presence of alien fish (Hayes and Jennings, 1986; Jennings, 1988b; Rosen et al., 1995; Kiesecker and Blaustein, 1998; Adams, 1999; Adams et al., 2003; Maret et al., 2006), commercial exploitation (Hayes and Jennings, 1986; Jennings and Hayes, 1985; Jennings, 1988b), disturbance regimes (Jennings and Hayes, 1994; Doubledee et al., 2003; Maret et al., 2006), diseases (Rosen and Schwalbe, 2002), and toxicants (Hayes and Jennings, 1986; Rosen et al., 1995; Davidson et al., 2002) can also be involved in declines of native species or interact synergistically to exacerbate bullfrog effects. This complexity frequently makes parsing the exact contribution of bullfrog predation to native-species declines problematic. Despite such complications, predation by bullfrogs has likely played a central role in declines of several native reptile and amphibian species in the western United States. It has been claimed that *R. catesbeiana* has led to decline of native *Rana* in the region around Florence, Italy (Touratier, 1992b) and of native fish in the Aquitaine of southwestern France (Touratier, 1992a), and concern has been expressed about their potential effects elsewhere in Europe (e.g., Albertini and Lanza, 1987; Stumpel, 1992). But in none of these cases has any of the above-mentioned forms of evidence been provided. Concerns have also been expressed about the potential threat of bullfrogs to the endangered snake *Opisthotropis kikuzatoi*, endemic to Kumejima Island, Ryukyu Islands, Japan. The threat comes both from the frog's potential to directly prey upon these small snakes but also because it is known to eat the endangered freshwater crab, *Candidiopotamon kumejimense*, the only known food source for the snake (Ota et al., 2004a).

Three of six dissected *Xenopus laevis* in an introduced population in southern California were found to contain one or more of the endangered tidewater goby (*Eucyclogobias newberryi*) as food items (Lafferty and Page, 1997). The high frequency of occurrence of the endangered fish in this small sample of stomachs, in concert with the high densities at which *X. laevis* can occur in California, led to the supposition that the alien frog might serve as a substantial cause of mortality for the fish (Lafferty and Page, 1997). However, further work to identify population-level

Table 3.1 Reported instances of alien reptiles or amphibians preying upon endangered or sensitive native wildlife

Alien predator	Native prey	Prey status	Location	Reference
<i>Anolis carolinensis</i>	<i>Cryptoblepharus nigropunctatus</i>	Restricted range	Ogasawara Islands	Suzuki and Nagoshi, 1999
<i>Anolis grahami</i>	<i>Eumeces longirostris</i>	Endangered	Bermuda	Griffith and Wingate, 1994
<i>Caiman crocodilus</i>	<i>Crocodylus rhombifer</i>	Endangered	Cuba	Varona, 1980
<i>Hemidactylus frenatus</i>	<i>Nactus coindemirensis</i>	Endangered	Mauritius	Cole et al., 2005
<i>Litoria aurea</i>	<i>Leiopelma archeyi</i>	Endangered	New Zealand	Thurley and Bell, 1994
<i>Python molurus</i>	<i>Neotoma floridana smalli</i>	Endangered	Florida, USA	D.U. Greene et al., 2007
<i>Python molurus</i>	<i>Aramus guarana</i>	Species of concern	Florida, USA	Snow et al., 2007b
<i>Python molurus</i>	<i>Endocimus albus</i>	Species of concern	Florida, USA	Snow et al., 2007b
<i>Rana catesbeiana</i>	<i>Ambystoma californiense</i>	Endangered	California, USA	Balfour and Stitt, 2003
<i>Rana catesbeiana</i>	<i>Ambystoma tigrinum stebbinsi</i>	Endangered	Arizona, USA	Maret et al., 2006
<i>Rana catesbeiana</i>	<i>Bufo nelsoni</i>	Restricted range	Nevada, USA	Jones et al., 2003
<i>Rana catesbeiana</i>	<i>Anas bahamensis</i>	Regionally rare	Puerto Rico	López-Flores et al., 2003
<i>Rana catesbeiana</i>	<i>Candidiopotamon kumejimense</i>	Endangered	Kumejima Is., Japan	Ota et al., 2004a
<i>Rana catesbeiana</i>	<i>Gallinula chloropus sandvicensis</i>	Endangered	Hawaii, USA	Viernes, 1995
<i>Rana catesbeiana</i>	<i>Gila purpurea</i>	Endangered	Arizona, USA	Schwalbe and Rosen, 1988
<i>Rana catesbeiana</i>	<i>Poeiliopsis occidentalis sonoriensis</i>	Endangered	Arizona, USA	Schwalbe and Rosen, 1988
<i>Rana catesbeiana</i>	<i>Thamnophis gigas</i>	Endangered	California, USA	Wylie et al., 2003
<i>Rana perzi</i>	<i>Alytes muletensis</i>	Endangered	Balearic Islands	Pleguezuelos, 2004
<i>Rana perzi</i>	<i>Gallotia galloti</i>	Restricted range	Canary Islands	Nogales et al., 1989
<i>Tupinambis teguixin</i>	<i>Eremochelys imbricata</i>	Endangered	Fernando de Noronha	Homewood, 1995
<i>Tupinambis teguixin</i>	<i>Caretta caretta</i> , <i>Chelonia mydas</i>	Endangered	Isla de San Andrés	Rueda-Almonacid, 1999
<i>Varanus niloticus</i>	<i>Athene cunicularia floridana</i>	Species of concern	Florida, USA	T. Campbell, 2005
<i>Varanus exanthematicus</i>	<i>Gopherus polyphemus</i>	Endangered	Florida, USA	Owens et al., 2005
<i>Xenopus laevis</i>	<i>Encyclogobias newberryi</i>	Endangered	California, USA	Lafferty and Page, 1997

effects of these frogs has not appeared. More compelling correlational evidence is available from France, where *X. laevis* was introduced in Deux-Sèvres in the mid-1980s (Fouquet, 2001; Fouquet and Measey, 2006). Amphibian communities in ponds containing *X. laevis* closest to the original site of introduction were found to have lower species richness and diversity than ponds lacking that frog or having it but occurring farther away (Grosselet et al., 2005). In this case, distance from introduction site is taken as a rough measure of duration of infestation with *X. laevis*; hence, long association with *X. laevis* is correlated with reduced native amphibian diversity. Numbers of eggs of native salamanders (*Triturus* sp.) were also approximately an order of magnitude lower in ponds containing *X. laevis* than in those lacking them. Finally, populations of *Triturus cristatus* from ponds containing *X. laevis* lacked the smaller size classes present in ponds without that frog (Grosselet et al., 2005).

It has been noted that populations of *Hyla squirella* and *H. cinerea* in a Florida hammock were found to decline dramatically upon colonization of the hammock by adult *Osteopilus septentrionalis* (Meshaka, 2001: 98). Although the mechanism of decline remains unidentified, it was presumed to be predation, given the known feeding habits of the alien.

Tadpoles of *Rana catesbeiana* were demonstrated to feed upon eggs and larvae of the endangered fish *Xyrauchen texanus* in laboratory conditions (Mueller et al., 2006), and their densities in artificial habitats (human-made levee ponds) can be sufficiently high that they may be depressing larval recruitment of the fish, but studies have not yet demonstrated direct impacts on fish in wild habitats. Tadpoles of *Osteopilus septentrionalis* have been demonstrated to prey upon and significantly reduce average survivorship of native *Hyla squirella* tadpoles under crowded laboratory experiments (K.G. Smith, 2005b) but not under conditions of moderate density and alternate food availability (K.G. Smith, 2005a).

Individual reports of alien reptiles or amphibians feeding on endangered or potentially sensitive native species have been reported (Table 3.1) but each of these reports is based on single or few observations, and depression of native populations has not been investigated. In other instances (Martínez-Morales and Cuarón, 1999; Enge et al., 2004c) reasonable concerns have been voiced over the potential for recent reptile introductions to impact endangered or sensitive native wildlife, but insufficient time has elapsed to validate these concerns. However, Martínez-Morales and Cuarón (1999) speculated that already-depressed populations of several endemic birds and mammals on Cozumel might be due to introduced *Boa constrictor*.

In sum, predation impacts from alien herpetofauna are frequently invoked and have been clearly demonstrated in a few instances. Anecdotal observations (Table 3.1) suggest they may be of frequent occurrence, but population-level effects are difficult to demonstrate and may be difficult to distinguish from other causes (witness bullfrogs in the western United States). There is an additional difficulty in that there is typically a narrow window of opportunity after an invasion begins during which predation impacts can clearly be demonstrated by direct observation and measurement. But this is precisely the stage of an invasion during which study is, in general,

least likely, either because the invasion is not noticed or because it is not perceived to be a concern. More often, the swiftness with which native prey can disappear makes hypotheses of predation impact merely liable to ex post facto inference instead of direct demonstration. Nonetheless, the numerous suggestive or compelling examples make it likely that population suppression via predation represents one of the more common ecological impacts from alien herpetofauna.

Removal of Native Predators

A second effect involves destruction of native predators via introduction of species bearing novel defensive mechanisms. This is documented for the cane toad (*Bufo marinus*), a Neotropical anuran that attains large size, defensively secretes quantities of highly toxic bufoteneins from its skin, and attains high population densities where introduced. It appears to have had dramatic effects on many native predators in its introduced range in Australia because of the naivety of native Australian predators to that species and its toxin. There are several reports of native snakes, lizards, turtles, crocodiles, birds, and mammals dying after ingesting toads (Breedon, 1963; Rayward, 1974; Covacevich and Archer, 1975; Stammer, 1981; Ingram and Covacevich, 1990; Shine, 1991; Tyler, 1994; S. Burnett, 1997; van Dam et al., 2002; Fearn, 2003; Phillips and Fitzgerald, 2004; Doody et al., 2006a) or experiencing population crashes or community changes subsequent to arrival of toads (Pockley, 1965; Shine and Covacevich, 1983; S. Burnett, 1997; McRae et al., 2005; Doody et al., 2006a, b; Shine et al., 2006). At least 26 native Australian vertebrate species have experienced such toad-induced mortality (C. Lever, 2001). These reports tend to be anecdotal or inferential but the studies by Doody et al. (2006a, b) contained pre-invasion abundance estimates for *Varanus panoptes*, *V. mertensi*, and *V. mitchelli* and demonstrated significant population declines synchronous with arrival of toads, as did the independent study of Griffiths and McKay (2007) for *V. mertensi*. B.L. Phillips et al. (2003), using ecoclimatic, dietary, and toxin-sensitivity information, systematically assessed risk to Australia's snake species from cane toads and concluded that 43% of Australia's non-scolecophidian snake fauna (i.e., excluding the burrowing blind snakes) are potentially threatened by the toads. Identical conclusions placing much of Australia's large herpetofauna at risk derive from a similar analysis for the remaining Australian taxa of large reptiles (J.C. Smith and Phillips, 2006).

Unpublished data suggest that some *Varanus* populations can survive invasion by cane toads (van Dam et al., 2002). In the invasion area studied, most *Varanus* consumed toads and were killed by doing so; however, those few lizards that survived the invasion did not eat toads, and this allowed for long-term recovery of lizard populations. *Varanus* from populations having long exposure to toads also refuse to attack toads (van Dam et al., 2002). Both these observations argue for strong selective pressure against toad consumption by some predatory lizards, which may lead to eventual recovery of native populations. However, further data

are needed to determine how general this result is across Australia's diversity of native predators, and no research has yet investigated the effect such strong selective pressure has had on genetic diversity within the varanid populations. Ecological studies at the expanding front of toad invasion in Northern Territory are underway (R. Shine, University of Sydney, personal communication, 2007), so more direct evidence of population-level effects may be forthcoming.

Bufo marinus were also introduced to Kayangel Atoll in Palau and to Ponape and Kosrae in the Federated States of Micronesia in a deliberate attempt to control *Varanus indicus*, which were considered undesirable because of their propensity to kill chickens (Gressitt, 1952; W.B. Jackson, 1962; Dryden, 1965). Introduction of *B. marinus* did result in a dramatic reduction of *Varanus* in Kosrae, with some dead monitors found with toads in their mouths (Dryden, 1965). The toads have been credited with apparent monitor declines on Guam (McCoid et al., 1994a), Ponape (W.B. Jackson, 1962), and Palau (Thyssen, 1988) as well. Similar results have been said to attend the introduction of toads to New Guinea (Pippet, 1975) and the Solomon Islands (Cain and Galbraith, 1957). Anecdotal reports of poisoning of native wildlife from ingestion of cane toads also come from Bermuda (Davenport et al., 2001) and Fiji (Gorham, 1968).

In laboratory experiments, eggs and larvae of *Bufo marinus* can be toxic to an array of native invertebrates and tadpoles (Crossland, 1998a, b; Crossland and Alford, 1998; Crossland and Azevedo-Ramos, 1999; Punzo and Lindstrom, 2001), and that toxicity can increase ontogenetically (Crossland, 1988b). In experiments carried out in artificial ponds, these results were extended to demonstrate that presence of *B. marinus* eggs and tadpoles significantly depressed survival of native *Limnodynastes ornatus* tadpoles, presumably via poisoning of the latter. This depression of *L. ornatus*, in turn, led to enhanced survival of native *Litoria rubella* tadpoles due to release from predation by the former (Crossland, 2000). Survival of *L. ornatus*, *L. tasmaniensis*, *L. terraereginae*, and *Notaden bennetti* was also sometimes depressed in independent pool and pond-enclosure experiments (Williamson, 1999). These results are suggestive of changes liable to occur in native anuran communities from introduction of *B. marinus*, but direct examination for similar effects under entirely natural circumstances has not occurred. Larval *B. marinus* can be toxic to a few native Australian fish species as well (Crossland and Alford, 1998; van Dam et al., 2002) but are typically rejected as food (Lawler and Hero, 1997; van Dam et al., 2002), so seem unlikely to exert any significant effects on native fish populations.

Wider Changes in Ecosystem Dynamics

The widespread loss of terrestrial vertebrates occasioned by the introduction of *Boiga irregularis* and other vertebrates to Guam led to ecosystem-wide trophic changes (Fritts and Rodda, 1998). The dominant vertebrate biomass on Guam now consists of alien species, there is an increased number of predatory links in the food

web, five ecological guilds previously present are now absent, and other ecological guilds have become rare (Fritts and Rodda, 1998). Wholesale loss of avian and mammalian insectivores has apparently resulted in an increase of spiders (Fritts and Rodda, 1998; Rodda et al., 1999b) and changes in their web-making behaviors (Kerr, 1993). The extirpation of volant frugivores has been predicted to lead to losses of pollinator and fruit-dispersal services to native plants, leading to long-term changes in floral composition (Savidge, 1987b); extirpation of insectivores is expected to increase damaging insect populations, leading to increased rates of herbivory on native plants (McCoid, 1991; Fritts and Rodda, 1998). Observations of slowed or failed regeneration in some plant populations (Perry and Morton, 1999; Ritter and Naugle, 1999) are consistent with these predictions, but other factors (especially high ungulate densities) are also involved, so conclusive evidence of those secondary effects is not yet available.

Secondary effects have been demonstrated to attend invasion of cane toads in northern Australia. Subsequent to arrival of the toads, monitor lizards (*Varanus panoptes*) suffered dramatic decline, apparently from preying on the toxic new arrivals (Doody et al., 2006). This removed the most significant source of nest predation on the river turtle *Carettochelys insculpta*, increasing its nest-success rate by 20%. Doody et al. (2006) hypothesized that similar secondary effects would benefit sea turtles and other native species subject to heavy predation from *V. panoptes*, potentially leading to a cascade of trophic effects as yet unstudied.

The success of *Boiga irregularis* on Guam illustrates an additional secondary ecological effect of considerable importance. Early expectations were that snake abundance would abate once its food source of native birds declined. However, that did not happen because the snake population is now maintained by supremely abundant alien vertebrate species, the most important of which are the lizards *Carlia ailanpalai*, *Hemidactylus frenatus*, and *Anolis carolinensis* (E.W. Campbell, 1996; Fritts and Rodda, 1998; McCoid, 1999; Rodda et al., 1999b, c). In this instance, the secondary effect is not from the snake itself but from the alien prey organisms that allow it to maintain high densities and continue cropping native prey to extinction. This effect from the alien prey base is maintained because the reproductive rates of the alien lizards far exceed those of the snakes (Fritts and Rodda, 1998), making them a reliably available resource.

A similar alien-prey boost to an invasive snake predator has been proposed elsewhere: high population densities of the alien frog *Rana perezi* on the Balearic Islands are thought to maintain high population densities of the alien snake *Natrix maura* (Moore et al., 2004a). This snake is thought to be the primary threat to the survival of the endangered endemic frog *Alytes muletensis* (Alcover et al., 1984; Tonge, 1986), and the latter is largely limited to rugged upland areas in which both *N. maura* and *R. perezi* are scarce (Moore et al., 2004a).

This augmentation of food resources for alien predators by alien reptiles and amphibians may be of more common occurrence than currently appreciated because many species of both taxa can attain tremendous population densities and biomass (Burton and Likens, 1975; Gosz et al., 1978; Rodda et al., 2001; Rodda and Dean-Bradley, 2002; Gibbons et al., 2006), including in their introduced ranges

(e.g., Greenlees et al., 2006; Woolbright et al., 2006). Thus, many reptile and amphibian species are likely candidates to facilitate subsequent alien predator establishment by serving as a dense food source. Concern has been expressed that this phenomenon could facilitate establishment of introduced snakes in Hawaii (Kraus et al., 1999; Kraus and Cravalho, 2001; Loope et al., 2001), but this form of ecological “priming” has been uninvestigated except for the *Boiga* and *Natrix* cases discussed above. As introductions of additional herpetological predators and their prey continue to increase this phenomenon may become more widely noticed.

Dense populations of alien reptiles and amphibians could potentially affect nutrient-cycling dynamics within ecosystems, but this effect has been little investigated to date. It has been proposed that two alien frogs (*Eleutherodactylus coqui* and *E. planirostris*) could serve as nutrient sinks in Hawaii by depletion of invertebrate biomass and disruption of ecological pathways (Kraus et al., 1999). This speculation was based on known high population densities of the frogs, their high invertebrate-cropping rates, and the lack of native predators (and paucity of alien predators) to feed on them. One study (Beard and Pitt, 2006) lent some support to this conjecture, finding that in a dense population of *E. coqui* frogs were consumed in very low amounts by mongoose (*Herpestes javanicus*) but not at all by rats (*Rattus rattus* and *R. exulans*) or cane toads (*Bufo marinus*). These are the only predators available to prey on these frogs in most of Hawaii. Studies in their native Puerto Rico have shown *E. coqui* to affect nutrient cycling dynamics in forest plots by reducing aerial invertebrates and leaf herbivory and by increasing primary productivity and leaf decomposition rates (Beard et al., 2002, 2003). These effects resulted from high predation rates on aerial insects and fertilization of soil by frog feces. Identical effects were found in the invaded range of *E. coqui* in Hawaii, as were reductions in numbers of herbivorous and leaf-litter invertebrates and increases in new leaf production by the invasive plant *Psidium cattleianum* in one invaded site (Sin et al., 2008).

Similar ecosystemic impacts are considered likely to result from the invasion of *Bufo marinus* in northern Australia. In this system, a four-fold increase in amphibian biomass has been documented as toads invade virgin territory (Greenlees et al., 2006). Because the toad is largely invulnerable to predation by native species, the increase in amphibian biomass is expected to serve as a nutrient sink (Greenlees et al., 2006), although possible effects on primary productivity and decomposition rates would also merit investigation.

Another change to community dynamics is attributed to colonization by *Bufo marinus*. High prevalence of a native tapeworm in the Australian anuran *Litoria pallida* declined after invasion by cane toads, apparently because the high density of toads interfered with transmission of the parasite to its definitive snake host, *Liasis childreni* (Freeland, 1994). The tapeworm’s life cycle originally involved transmission of eggs from snake feces to frogs via consumption of infected food. Cyst-bearing frogs were then consumed by the snakes, completing the worm’s life cycle. The creation of high-density populations of voracious toads shunted most worm eggs to that alien species, which was shunned as a food item by the snakes, breaking the life-cycle of the tapeworms and reducing their prevalence in native

frog populations. The tapeworm's decline has been associated with a decline in the stability of the local frog community (Freeland, 1994).

Each of these documented or potential changes to food webs and ecosystem dynamics stems directly from the high standing biomass that some alien reptiles and amphibians are capable of achieving. Direct measurements of biomass or densities have not often been made for alien populations of reptiles and amphibians. However, there is a number of herpetological genera with naturalized populations whose densities are sufficiently high that they are likely candidates for disrupting trophic dynamics of invaded ecosystems. These include frogs of the genera *Bufo*, *Eleutherodactylus*, *Osteopilus*, *Rana*, and *Xenopus* and lizards of the genera *Anolis*, *Carlia*, *Chamaeleon*, *Hemidactylus*, *Lampropholis*, and *Podarcis*. This list is not exhaustive but merely highlights some of the more promising taxa for investigation.

Competition with Native Species

As noted above, *Bufo marinus* has depressed reproductive success of rainbow bee eaters partially through competition for burrow use (Boland, 2004a). Tadpoles of the same species also depressed growth rates among a variety of native anuran larvae in pool and pond-enclosure experiments, but inconsistency among trials leaves unanswered the extent to which competition exerts population-level effects among tadpoles in natural settings (Williamson, 1999). Other experiments indicated apparently strong competitive effects between *B. marinus* tadpoles and those of *Limnodynastes ornatus* (Crossland, 1997, cited in van Dam, 2002). No competitive effect was noted between adult toads and native frogs (Freeland and Kerin, 1988).

The expansion of *Eleutherodactylus johnstonei* across the Lesser Antilles has been correlated with the decline or replacement of native congeners on several islands (Hardy and Harris, 1979; H. Kaiser and Henderson, 1994; H. Kaiser et al., 1994; H. Kaiser, 1997). However, this replacement largely goes hand in hand with habitat destruction: *E. johnstonei* has a greater physiological tolerance for higher temperatures and drying (Pough et al., 1977) and greater use than native *Eleutherodactylus* of opened habitats (Stewart, 1977; Stewart and Martin, 1980). This tolerance seems to facilitate its use of expanding areas of vegetation disturbed by human activities (H. Kaiser, 1997), apparently at the occasional expense of resident congeners (Hardy and Harris, 1979; H. Kaiser, 1997).

Competitive effects from larval *Rana catesbeiana* can be varied. They depress growth rates and survival in larval *R. boylei* owing to exploitative competition for algal resources (Kupferberg, 1997a). They also inhibit growth rates in larval *R. aurora* by passive exclusion under conditions in which food resources are clumped (Kiesecker et al., 2001). This happens because larval *R. aurora* avoid tadpoles of *R. catesbeiana* and, hence, lose access to the clumped food resources around which the latter invariably gather (Kiesecker et al., 2001). The two mechanisms need not be exclusive: exploitative deficiencies of native *Rana* tadpoles may

be worsened by also decreasing activity levels (and, hence, amount of time spent feeding) in the presence of *R. catesbeiana* (Kiesecker et al., 2001). Severity of competitive effects may vary with environmental conditions between aquatic habitats (Adams, 2000), a confounding factor that has yet received no detailed treatment. Laboratory trials have also found survival of native European *Rana* tadpoles to be considerably reduced in the presence of larval *R. catesbeiana*, even when densities of the latter were low (Laufer and Sandte, 2004). This appeared to result from direct competition for food inasmuch as larval bullfrogs displaced native tadpoles from food resources and larval predation was never observed.

Similar competitive effects have been found with *Osteopilus septentrionalis* introduced to Florida. Tadpoles of this species depressed growth rates and delayed metamorphosis in native *Bufo terrestris* and *Hyla cinerea* when raised together in a laboratory setting; they also led to reduced size at metamorphosis in *B. terrestris* (K.G. Smith, 2005a). When raised together in mesocosm experiments *O. septentrionalis* decreased survival rates, growth rates, and size at metamorphosis of *B. terrestris*, although those effects were reversed when tadpoles were raised in the presence of predatory newts (*Notophthalmus viridescens*), which preferentially preyed upon the alien tadpoles (K.G. Smith, 2006b). Although these results are suggestive, competitive impacts of *O. septentrionalis* in natural systems remain experimentally uninvestigated.

Pearl et al. (2005b) documented unexpectedly frequent rates of interspecific amplexus between *Rana catesbeiana* and native *R. aurora* and *R. pretiosa* in the Pacific Northwest of the United States. They hypothesized that, should males of the two natives be limited in breeding pools, sexual interference by frisky *R. catesbeiana* might serve as a hindrance to population recruitment, although the importance of such a mechanism remains to be demonstrated.

A variety of alien lizards has been presumed to competitively displace native species, judging from historical patterns of changes in species abundance and geographical patterns of species assortment (Case and Bolger, 1991; Case et al., 1994). Exclusion of the long-resident geckos *Lepidodactylus lugubris* by recently established *Hemidactylus frenatus* in urban and suburban niches in several locations in the Pacific appears to result from behavioral interference (Bolger and Case, 1992) and consumption of juveniles by the newcomer (Bolger and Case, 1992; McCoid and Hensley, 1993b), but especially by enhanced ability of *H. frenatus* to exploit food resources (Petren and Case, 1996). This exploitative exclusion is dependent upon dense concentrations of insects attracted to human light sources and the structural simplicity of building surfaces (Petren et al., 1993; Petren and Case, 1998). However, *L. lugubris* also avoid *H. frenatus* (Bolger and Case, 1992; S.G. Brown et al., 2002), and this avoidance may make *L. lugubris* more susceptible to predation subsequent to invasion by *H. frenatus* (S.G. Brown et al., 2002). Although *L. lugubris* itself may be a human introduction across much of the Pacific (Moritz et al., 1993), making this an example of displacement of one alien lizard by a more recent introduction, it does illustrate the potential for competitive exclusion to result from alien lizard introductions. A similar mechanism may be occurring between two alien geckos in Texas. There, resident *H. turcicus* are being displaced by more recently arrived *Cyrtopodion scabrum*, and the displaced species exhibits a dietary shift in sympatry that is consistent with strong

dietary competition (Klawinsky et al., 1994). Both displacement and dietary shift may be mediated by interference competition for perch sites, which has been demonstrated in enclosure experiments (Vaughan et al., 1996). However, in laboratory experiments, Dame and Petren (2006) demonstrated that replacement of *Hemidactylus garnotii* across the Pacific by *H. frenatus* cannot be explained by either resource competition or aggression, leaving uncertain what mechanism is responsible.

Clearer evidence attends the competitive exclusion of endemic and highly endangered *Nactus* species in the Mascarene Islands by invasive *Hemidactylus frenatus*. In this situation it is known that the endemic geckos *N. coindemirensis*, *N. durrelli*, and *N. serpensinsula* have disappeared across most of Mauritius and its satellite islets, being confined (with one exception) only to a few islets lacking *H. frenatus* (Arnold and Jones, 1994; Cole et al., 2005). Outdoor enclosure experiments have shown *H. frenatus* to aggressively interact with individuals of the smaller *Nactus* species, displacing them from daytime refugia, injuring some individuals, and preying upon others (Cole et al., 2005). Competitive exclusion from refugia presumably makes the native geckos more susceptible to predation by invasive mammals like cats and rats, and injury is likely to directly impact survival of affected individuals. The native geckos persist only in a few small areas having substrates not easily negotiated by the alien.

The skink, *Cryptoblepharus nigropunctatus*, endemic to the Ogasawara Islands, has been reported to be declining on Chichijima since the late 1970s, and by the 1990s the skink could not be found in areas having high densities of introduced *Anolis carolinensis* (Miyashita, 1991; Suzuki and Nagoshi, 1999). This appears to result from direct competition with *A. carolinensis*. Where the two occur syntopically, there have been changes in substrate use and perch height by *Cryptoblepharus*, suggesting that competition for favorable basking sites may explain some of the native lizard's displacement. Further, *Anolis* were invariably observed to attack *Cryptoblepharus* when food was experimentally presented between pairs of each species in the wild (Suzuki and Nagoshi, 1999). Both results suggest that interference competition by the larger alien lizard is causing the decline of the native.

It has been observed that *Carlia ailanpalai*, introduced to the Mariana Islands, is extremely aggressive toward the native terrestrial lizards, attacking them, stealing their food, and possibly preying on them (Rodda et al., 1991; McCoid, 1995b). It has been proposed that this aggressive behavior may serve as a competitive exclusion mechanism contributing to the decline or disappearance of several populations of native skink in the region (Rodda et al., 1991; Rodda and Fritts, 1992; McCoid, 1995b). This hypothesis is reasonable but has yet to be experimentally tested.

Podarcis wagleriana is native to Sicily and the satellite Aegadian Islands; *P. raffonei* is a close relative restricted to some of the nearby Aeolian Islands (Capula, 1994a). *Podarcis sicula* is native to mainland Italy, Sicily, and Adriatic coastal areas but has been introduced on some islands in the native ranges of *P. wagleriana* and *P. raffonei* (Capula, 1992, 1994b). In those circumstances, *P. sicula* either dominates or replaces the native lizards. This has been argued to reflect competitive superiority because the alien lizard predominates in virtually all available microhabitats (Capula, 1992). Genetic (Capula, 1993) and distributional (Capula, 1992) evidence suggest that this

competition has led to extirpation of *P. raffonei* throughout most of its original range, and the species is now virtually extinct (Capula et al., 2002).

The replacement of *Anolis carolinensis* in Florida by invasive *A. sagrei* may be due in part to competitive effects on reproduction. In enclosure experiments, female *A. carolinensis* laid fewer eggs when placed in sympatry with *A. sagrei* than when housed alone or (sometimes) with conspecifics (Vincent, 1999). In contrast, *A. sagrei* females did not reduce reproductive output in sympatry with *A. carolinensis*. Whether such results also obtain in the field remains unknown but, if so, would complement the effects of hatchling predation by *A. sagrei* discussed earlier.

Concern has been raised about alien *Trachemys scripta* competing with native *Emys orbicularis* in Europe (Frisenda and Ballasina, 1990; Servan and Arvy, 1997; Arvy and Servan, 1998; Gianaroli et al., 1999), and they have been argued to act aggressively toward the native turtle and displace it from basking sites (Kaltenegger, 2006). Cadi and Joly (2004) demonstrated weight loss and reduced survival of *E. orbicularis* when confined with *T. scripta* in outdoor enclosures in southeastern France. Data from these same enclosures suggest this effect is at least partly due to superior competitiveness of *T. scripta* for basking sites, relegating *E. orbicularis* to poorer-quality sites (Cadi and Bertrand, 2003; Cadi and Joly, 2003). This effect was not due to active displacement of *E. orbicularis* by *T. scripta*, but simply resulted from its earlier occupation of basking sites during the morning and the reluctance of *E. orbicularis* to climb onto sites already occupied. Competition for basking sites has also been posited as a likely impact of *T. scripta* on native *Actinemys marmorata* in California (Spinks et al., 2003) and is consistent with earlier data showing behavioral avoidance of the alien turtle by that same population of *A. marmorata* (Holland, 1994). Impacts on wild populations of *E. orbicularis* have not been demonstrated but may be feasible, considering the rare status of that species in many localities and the densities which the alien turtle can attain (Cadi and Joly, 2003). This supposition needs to be tempered, however, with recognition that *T. scripta* exhibits low reproductive success and juvenile survival in much of Europe (Luiselli et al., 1997). If that observation holds generally, *T. scripta* populations may undergo attrition as adults die but fail to be replaced by additional pet releases because of the European Union's import ban on this species. So the practical effects of *T. scripta* for native turtle populations in Europe remain uncertain.

Enclosure experiments have also shown that female *T. scripta* gain a competitive edge over native *Chrysemys picta* females in Ohio, United States, by being more aggressive (McKenna and Tramer, 2001). Males of the two species did not exhibit such differences. Growth of *C. picta* was not affected by this behavioral difference but it seemingly led to an increased tendency of female *C. picta* to disperse away from the *T. scripta* (McKenna and Tramer, 2001).

Vectoring Novel Parasites

The pathogenic fungus *Batrachochytrium dendrobatidis* induces a recently emerged disease, chytridiomycosis, that has caused drastic declines and extinctions of many

species of amphibians worldwide (Berger et al., 1998; Daszak et al., 1999, 2003; Speare and Berger, 2000; Garner, 2005; Lips et al., 2006; Skerratt et al., 2007). Earliest known presence of this fungal infection is from the frog *Xenopus laevis* in Africa, and this suggests that the fungus may have begun its global spread with the widespread export (resulting in frequent release) of *X. laevis* for laboratory and pregnancy testing in the 1930s (Weldon et al., 2004). Infection in *X. laevis* is typically asymptomatic (Weldon, 2004), as it is in the American bullfrog, *Rana catesbeiana* (Mazzoni et al., 2003; Daszak et al., 2004). This latter frog has been widely exported, farmed for food, and escaped or released into the wild in a large number of countries (Bury and Whelan, 1984); and *Batrachochytrium* has been documented in feral bullfrog populations in many parts of its introduced range (Hanselmann et al., 2004; Garner et al., 2006). Both alien frogs are, hence, efficient potential vectors of the fungus to naive, native frog faunas, and current evidence suggests their widespread transportation and release may be a contributing source to the global explosion of the disease in the past two decades. Consistent with this hypothesis is that the first documented occurrence of *Batrachochytrium* in Great Britain is at a site in Kent having the only breeding population of *R. catesbeiana* in the country, as well as a feral population of *X. laevis* (Cunningham et al., 2005; Fisher and Garner, 2007). Although movement of these two species may have been responsible for starting and abetting this amphibian pandemic, it is clear that a large number of widely traded amphibians can serve as vectors for *Batrachochytrium* and that the amphibian trade generally, whether leading to feral introductions or not, must be viewed as highly inimical to the continued persistence of uninfected amphibian faunas (Fisher and Garner, 2007).

Daszak et al. (1999) pointed out the likelihood that other amphibian disease organisms besides *Batrachochytrium* have been transported with the widespread introduction of alien bullfrogs and cane toads, but this reasonable supposition remains uninvestigated. However, iridoviruses of the genus *Ranavirus* have been implicated in numerous amphibian mortality events across North America in the past decade (Green et al., 2002; Jancovich et al., 2005), and genetic evidence suggests these viruses to have been derived from widely introduced sport fish, with subsequent spread across western North America due to the common use (and escape or release) as fish bait of alien larval *Ambystoma tigrinum* (Jancovich et al., 2004). Outbreaks of disease caused by *Ranavirus* affect a diversity of frog and salamander species, including some endangered forms (Jancovich et al., 1997).

At least one protozoan has been vectored to Australian frogs by introduction of *Bufo marinus*, and it has been able to expand to areas beyond the invasion front of the toad (Delvinquier, 1986; Delvinquier and Freeland, 1988a). Effects on native anurans are unknown. A variety of other protozoan parasites has arrived with *B. marinus* from its native range but are not yet known to infect native amphibians (Delvinquier and Freeland, 1988). Vectoring of alien helminths to new hosts via introduced lizards has been documented in Hawaii (Goldberg and Bursey, 2000a; Goldberg et al., 2004c), but effects on native taxa are non-existent because Hawaii lacks native lizards. These examples demonstrate the potential for introduced

reptiles and amphibians to transport new parasites to naive herpetofaunas, but whether this potential has translated into damage to native herpetofaunas is totally uninvestigated.

Observations of epidemic mortality events caused by viral or mycoplasma agents in *Actinemys marmorata* in California and Washington states, United States, were noted to have occurred in populations into which alien species of turtles had previously been introduced (Holland, 1994). This led to the reasonable hypothesis that the alien turtles served as vectors of a new disease agent into these populations. This speculation could not be directly tested but was consistent with the frequent maintenance of pet-store turtles under crowded and unsanitary conditions, which could easily allow for rapid acquisition of novel disease agents prior to a turtle escaping or being released (Holland, 1994).

Under somewhat more controlled circumstances, a total of 29 species of alien ticks has been imported into the United States on captive reptiles (BurrIDGE and Simons, 2003), and at least seven of these have established breeding populations at captive reptile facilities (S.A. Allan et al., 1998; BurrIDGE et al., 2000a; Simmons and BurrIDGE, 2000, 2002). One alien tick, *Amblyomma rotundatum*, has been found on feral *Bufo marinus* in Florida, which is presumed to have served as the vector to that new locale (Oliver et al., 1993). That tick has a broad host range in its native Central and South America but has not yet been reported from native wildlife in Florida. Another species, *A. dissimile* is also established in Florida, is thought to have arrived on imported reptiles, and has been found infecting native reptiles (Bequaert, 1932). It continues to arrive on imported reptiles from Central and South America (BurrIDGE and Simons, 2003). Several of these alien ticks are readily capable of switching onto hosts to which they have no prior history of exposure (BurrIDGE, 2001), suggesting a capability to infect native reptile species. The potential for this wide array of ticks to vector diseases to native reptile and amphibian populations has been largely uninvestigated, but two of these tick species can vector reptilian haemogregarines, and severe infestations of one species have led to respiratory distress and death in some reptiles (BurrIDGE, 2001). The finding of lethal infections of the tick-vector *Ehrlichia ruminantium* or a close relative in a phylogenetically varied array of captive snakes suggests that risks to native reptiles are potentially serious (Kiel et al., 2006); however, this potential remains unexamined in wild populations.

Community Homogenization

Little attention has yet been paid to the broader-scale effects that accumulating introductions have for homogenization of herpetological communities. One exception is a recent investigation into regional changes in herpetological communities attending alien introductions to Florida. This study found that introductions made to date have increased homogenization of communities at the small spatial scale of adjacent counties but had not yet shown a similar tendency toward homogenization

across the state as a whole (K.G. Smith, 2006a). This spatial contrast probably results from two factors: the recency of many introductions has likely not yet allowed homogenization effects to spread very far, and the climatic gradient in peninsular Florida may not allow many established southern species to access more northerly latitudes. This is the only study I know to quantify regional effects of herpetological introductions.

Evolutionary Effects

Evolutionary effects from invasive reptiles and amphibians are primarily of interest in terms of how they impact native faunas. Such effects have been demonstrated in a few cases, are frequently to be expected, but have been little studied to date. Evolutionary changes have been noted for the alien invaders themselves in a few instances. With the possible exception of the last example below, all changes discussed here have or are presumed to have a genetic basis.

Genetic Changes

Hybridization with congeners is a frequent outcome of rampant transport of organisms (cf., Levin et al., 1996; Rhymer and Simberloff, 1996; Mooney and Cleland, 2001; Low, 2003: 261–272; Largiadèr, 2007), and the same consequence has been documented for a number of alien reptile and amphibian introductions. Such hybridization may lead to loss of native allelic or genomic identity, outbreeding depression (Rhymer and Simberloff, 1996), or, in the extreme case, loss of native species due to wholesale genetic swamping by the invader (e.g., Echelle and Connor, 1989). Clearly detrimental impacts on native reptiles and amphibians resulting from introgressive hybridization of alien genomes have been demonstrated for only a small set of species. Nonetheless, these effects have frequently been grave and this seems one of the more damaging impacts attending herpetological introductions.

Among amphibians, populations of the salamander *Ambystoma tigrinum* across the western United States have experienced widespread introduction of larvae of eastern forms of this species used as fishing bait (Lowe, 1955; Espinoza et al., 1970; Bury and Luckenbach, 1976; Collins, 1981). Genetic contamination of native populations has been documented in Arizona, where genetic introgression threatens the endangered *A. t. stebbinsi* (Storfer et al., 2004), and in California, where the endangered *A. californiense* is extensively threatened with the same (Riley et al., 2003). In the latter case, hybridization appears to be promoted by habitat alteration, with alien alleles preponderating in unnatural, perennial ponds. This pattern derives from differential success of hybrid genotypes and has resulted in a complex mosaic hybrid zone (Fitzpatrick and Shaffer, 2004).

The alien newt *Triturus carnifex* has introgressed with native *T. cristatus* in both Great Britain (Brede et al., 2000) and the Geneva Basin of Switzerland and France (Arntzen and Thorpe, 1999). In the former case, evidence of introgression is still limited to the introduction site. In the latter, the alien has largely replaced the native across the landscape over a period of 30–40 generations, although it is not clear whether this is due to introgression, competition, habitat degradation, or a combination of all three.

Hybridization threatens native bisexual and hybridogenic complexes of water frogs (*Rana* spp.) in Europe. *Rana* kl. *grafi* is a hybridogenic lineage that occupies northeastern Spain and southeastern France and originated from the hybridization of *R. ridibunda* with either *R. perezi* or the hybridogenic *R. kl. esculenta* (Pagano et al., 2001a, c). This lineage is maintained by the standard hybridogenic mechanism of destruction of one parental genome prior to meiosis followed by backcrossing to one or the other parental species to re-form either a new generation of similar hybrids or reconstituted individuals of the parental species. Several of these hybridogenic lineages (or kleptons, designated by “kl.”) occur across Europe, involving a number of different parental species and their resultant hemiclinal classes (Graf and Polls Pelaz, 1989; Günther, 1990; Pagano et al., 2001a; Arnold and Ovenden, 2002). Alien *R. ridibunda*, *R. lessonae*, and *R. kl. esculenta* have been recently introduced to Spain, are hybridizing with the native *R. perezi*, and are introgressing foreign genes into the local complex of water frogs (Arano et al., 1995). It is thought that this poses a threat to the bisexual *R. perezi* by boosting heterozygosity values in local hybridogenic *R. kl. grafi*, which may then outcompete *R. perezi*. Similar fears attend the introduction of the alien *R. kl. esculenta* (Arano et al., 1995). Although the feared displacement mechanism, strictly speaking, is competition, the system could not be maintained without the successful introduction of the alien genomes; hence, continued hybridization is key to the threat. Similarly, in Switzerland, hybridization of alien *R. ridibunda* with native *R. lessonae* and native *R. kl. esculenta* has led to creation of, respectively, additional numbers of *R. ridibunda* and new genotypes of *R. kl. esculenta*, which themselves are capable of producing additional generations of *R. ridibunda* by backcrossing with the alien frogs (Vorburger and Reyer, 2003). These new genomic combinations have contributed to the rapid replacement of the two native water frogs by *R. ridibunda* during the past half century (Vorburger and Reyer, 2003). The standard mechanism for maintaining hybridogenesis does not involve meiotic recombination, although such does occasionally occur (Pagano and Schmeller, 1999). In southern France, introduction of alien water frogs has also led to introgression of foreign genes into local water frog gene pools (Pagano and Schmeller, 1999; Pagano et al., 2003) as well as creation of novel assemblages of water frog genomes that were previously absent (Pagano et al., 2001c). The potential for similar genetic pollution elsewhere in the ranges of these hybridogenic water frog complexes is obvious.

As mentioned earlier, *Podarcis wagleriana* is native to Sicily and the satellite Aegadian Islands and *P. raffonei* to the nearby Aeolian Islands (Capula, 1994a). On some of these islands, the introduced *P. sicula* has been documented to hybridize with the native – with *P. wagleriana* on Marettimo and with *P. raffonei* on Vulcano

(Capula, 1993). These events have led to some genetic introgression on each island, and evidence indicates there was hybridization with *P. raffonei* prior to its extinction on Lipari as well (Capula, 1993). To what extent genetic introgression has contributed to the decline of *P. raffonei* beyond that attributed to the competitive effects noted earlier remains unknown.

Hybridization between *Iguana delicatissima* and *I. iguana* is documented and is argued to be contributing to the displacement of the former in Guadeloupe and les Îles des Saintes (Day and Thorpe, 1996; Day et al., 2000; Breuil, 2000a, b, 2002). It remains uncertain that *I. iguana* is alien to this region but it highlights the potential for similar problems in nearby areas (e.g., northern Lesser Antilles) where it certainly is not native.

Some populations of *Anolis distichus* may originally have been native to Florida (L.D. Wilson and Porras, 1983, but see A. Schwartz, 1968a for a contrary opinion) and were given the designation *A. d. floridanus* (H.M. Smith and McCauley, 1948). But three other subspecies of *A. distichus* have been introduced to Florida (W. King and Krakauer, 1966; Bartlett, 1995a), and hybridization between one of these, *A. d. dominicensis*, and the presumptive native has been sufficient to largely obliterate the distinctiveness of the latter, creating instead a continuum of phenotypes having no geographic structure (Miyamoto et al., 1986). Mitochondrial DNA evidence also supports a history of extensive hybridization among three or four lineages of *A. distichus* in this region (Kolbe et al., 2007a). Thus, the original population of *A. distichus* inhabiting Florida in the 1940s is now extinct and replaced by a variable hybrid swarm of largely alien composition. Whether this represents loss of a unique lineage or not is unknown.

Hybridization between native *Anolis carolinensis* and alien *A. porcatus* has also occurred in southern Florida (Kolbe et al., 2007a), but the magnitude of any genetic impact on the native remains unknown.

Hybridization with introduced *Trachemys scripta* may be a threat to the endemic *T. stejnegeri malonei* of Great Inagua Island (Mealey et al., 2002). If one believes the argument of Lee and Ross (2001) that *T. terrapin* is native to Grand Bahama Bank and not to Jamaica, the same threat would be posed by introduced *T. scripta* and *T. stejnegeri* on the islands of that bank (Lee, 2004, 2005), where hybrid swarms have resulted from past introductions (Seidel and Adkins, 1987; Seidel, 1988). Alien *T. scripta elegans* are widely hybridizing with native *T. scripta scripta* in Florida (Bartlett and Bartlett, 1999; Aresco and Jackson, 2006) and Virginia (Mitchell, 1994), but the degree of genetic pollution in these populations is not yet quantified. Introduced *Cuora flavomarginata* interbreed with the native species *Geoemyda japonica* in the Ryukyu Islands, and hybrids are moderately frequent on the same island between native *Protobothrops flavoviridis* and the introduced *P. elegans* (Nishimura and Akamine, 2002; Ota, 2002d; Ota and Hamaguchi, 2003). In both cases, the genetic integrity of the natives may be threatened by interbreeding with closely related aliens. Alien subspecies and DNA haplotypes of *Emys orbicularis* have been widely distributed around much of Europe (Lenk et al., 1998; U. Fritz et al., 2004), posing the threat of genetic contamination or swamping of local populations (Kaltenegger, 2006).

Genetic changes can also occur in the introduced species itself. The clearest example is for *Anolis sagrei*, native to Cuba, the Bahamas, and the coast of northern Central America and introduced to a variety of other localities. In Florida, *A. sagrei* was introduced at least eight separate times. These introductions were from a variety of localities in the native range of the lizard and this resulted in genetic diversity within Florida populations greatly exceeding that available in native populations (Kolbe et al., 2004, 2007b). This increased genetic diversity has been retained to a diminished extent in further populations in Grand Cayman Island, Hawaii, Louisiana, Taiwan, and Texas founded by animals from Florida, and it is thought to be one of the reasons for the success of *A. sagrei* in these several invaded localities (Kolbe et al., 2004, 2007b). Similar admixture of native genomes by multiple introductions has been shown for a number of other *Anolis* species introduced to Florida and the Dominican Republic (Kolbe et al., 2007a). Chuckwallas (*Sauromalus* spp.) found on Alcatraz, Sonora are claimed to be a hybrid swarm involving the three introduced species *S. ater*, *S. hispidus*, and *S. varius* (Case, 1982; Petren and Case, 1997; Mellink, 2002), although evidence for this assertion has not been published. More often, a decrease in genetic diversity (the so-called “founder effect”) is expected to obtain in most alien populations, reflecting their founding from very few individuals, each containing only a limited sample of the species’ total genetic diversity. Such reduced genetic variation has been observed within some populations of alien reptiles (Gorman et al., 1978) and can also serve to set the introduced population on a different evolutionary track from its parental species. So are novel genetic entities created by the process of human introduction.

Morphological Changes

Morphological changes in head shape and body size have been documented in two species of ranivorous Australian snakes, *Dendrelaphis punctulatus* and *Pseudechis porphyriacus*, with degree of change correlated with duration of exposure to invasive populations of cane toads, *Bufo marinus* (Phillips and Shine, 2004). Both snakes are highly sensitive to toad toxins, and observed morphological changes are toward reduced gape size and increased body size, in accordance with predictions for minimizing size-dependent vulnerability to toads (Phillips and Shine, 2006b).

The toads themselves have also changed morphologically through time, with reduction in body size and parotoid gland size both being negatively correlated with time since establishment of different populations (Phillips and Shine, 2005, 2006c). These changes presumably result from the high costs of producing large bodies and large quantities of toxin in novel environments in which they are unnecessary (Phillips and Shine, 2005), but response to climatic and seasonal variables is also involved (Phillips and Shine, 2006c). Furthermore, toad leg lengths have increased with time, giving a colonization advantage to longer-legged individuals, and

dramatically increasing the rate at which toads are expanding their range in Australia (Phillips et al., 2006).

Microevolutionary changes in morphometric and scale-count variables have occurred in Floridian populations of the alien *Anolis sagrei* (J.C. Lee, 1985, 1987), and these changes are the side-effect of novel admixing of independently introduced genomes from different parts of the species' native range (Kolbe et al., 2007b).

Physiological Changes

Australian snakes of the species *Pseudechis porphyriacus* are sensitive to toxin from introduced *Bufo marinus*. Snakes from populations exposed to toads for several decades have developed some degree of toxin resistance compared to conspecifics from toad-naive populations. This is not an individually acquired trait, and so must involve evolutionary adaptation of exposed populations to the toxin (Phillips and Shine, 2006a).

Behavioral Changes

Australian snakes of the species *Pseudechis porphyriacus* from populations exposed to toads for several decades have developed a non-learned aversion to eating the invasive *Bufo marinus* compared to conspecifics from toad-naive populations (Phillips and Shine, 2006a).

Native *Alytes muletensis* tadpoles, endemic to Mallorca, respond to chemical (and perhaps visual) cues from alien *Natrix maura* snakes by decreasing their activity levels, both in native plunge pools as well as under laboratory conditions (Griffiths et al., 1998). Post-metamorphic individuals show the same avoidance of snake chemical cues (Schley and Griffiths, 1998). Tadpole responses are specific to snake cues from the introduced population of *N. maura* on Mallorca and do not extend to conspecific snakes from the Iberian Peninsula (Griffiths et al., 1998). Use in these tests of captive-reared *A. muletensis* naive to snakes shows that behavioral responses are genetic and most likely acquired since the introduction of *N. maura* to the Balearic Islands approximately 2,000 years ago. Morphological changes in tadpole shape are also inducible by exposure to *N. maura* chemical cocktails, with exposed tadpoles developing longer tails with deeper musculature and shallower ventral fins (Moore et al., 2004b). This developmental plasticity again seems to have evolved in response to the introduction of *N. maura* (Moore et al., 2004b).

Similarly, tadpoles of native *Rana aurora* derived from ponds inhabited by alien *R. catesbeiana* show increased antipredator behavior and higher survival rates when exposed to *R. catesbeiana* in captivity than do tadpoles from evolutionarily naive populations (Kiesecker and Blaustein, 1997). Learning could be ruled out as a mechanism because tadpoles were derived from collected egg masses and, hence,

were individually naive to bullfrogs. Thus, behavioral avoidance appears to have a genetic basis. Juvenile *Pseudacris regilla* from ponds inhabited by *R. catesbeiana* also showed avoidance of chemical cues from the latter species, whereas juveniles from ponds lacking the alien frog did not (Chivers et al., 2001). In this last case, although evolution of avoidance behavior may be involved, the study design did not exclude the possibility of learning.

Until the extirpation of most birds and mammals from Guam brown treesnakes were primarily nocturnal in behavior. With the loss or extreme depletion of these nocturnal food sources during the 1980s, the snakes switched to largely feeding on diurnal lizards, and that prey switch is reflected in a major change in activity patterns for the snakes, with diurnal activity approaching 50% of all snake activity in the 1990s (Fritts and Rodda, 1998). Similarly, prior to 1988 the brown treesnake was primarily arboreal in behavior; during the 1990s, ground-level activity became the mode for some populations on Guam (Rodda, 1992b; Fritts and Rodda, 1998). It is uncertain whether these changes have a genetic basis or merely represent behavioral plasticity in the species. The latter seems more likely but it does highlight the degree to which behaviors that are thought to be typical for a species (in this case arboreality and nocturnality) may change in short order as circumstances require.

Social Effects

Economic

Economic effects from alien herpetofauna have been little considered, but those of the brown treesnake in Guam have been recognized as considerable. From 1978–1997, this species caused >1,600 power outages on Guam (Fritts et al., 1987; Fritts and Chiszar, 1999), including many of island-wide scope. Incurred costs are conservatively estimated to be from US\$1–4 million/year (United States Geological Survey, 2007) and include (1) damage to electrical-distribution equipment, (2) increased maintenance and emergency-repair costs, (3) damage to electrical products due to voltage surges, (4) loss of revenues during outages, (5) loss of business by consumers during outages, and (6) investment in backup generators and transformers to ensure stable power availability (Savidge, 1987b). Occasionally, power outages have resulted in loss of water to some parts of the island for periods up to one week (Savidge, 1987b). Outage durations have risen from an average of 1 hour every 3–4 days in 1997 to 1.5 hour every two days in 2003 (Burnett et al., 2006). Power outages on a very localized level have also been attributed to Cuban treefrogs (*Osteopilus septentrionalis*) taking refuge in transformers in Florida (S. Johnson, University of Florida, personal communication, 2007), but no quantification of costs is available.

Brown treesnakes are significant predators of domestic chickens and their eggs on Guam. Although the dollar value of this predation was not determined, approximately 80% of chicken farmers surveyed reported predation, and 45% of

these attributed predation to snakes (Fritts and McCoid, 1991). Fritts and McCoid (1991) concluded that brown treesnakes were an apparent factor contributing to Guam's inability to produce sufficient quantities of eggs for local consumption, leading to high-cost import substitution of eggs from Australia and the United States. As well as reducing the viability of a commercial poultry industry, increases in agricultural insect pests attributed to the snake's extirpation of insectivorous birds is argued to be partly responsible for Guam's agricultural decline since 1945 (United States Geological Survey, 2007). The snake also takes a toll on pets, primarily puppies and cage birds, but the cost of this loss is unestimated (Rodda and Savidge, 2007). Total costs of brown treesnakes to the United States have been estimated at US\$12 million/year (Pimentel et al., 2005), which includes damage costs on Guam and funds expended to control the species and prevent its further introduction elsewhere.

Poultry depredation has also been reported for *Varanus indicus* in Guam (Crampton, 1921; Fritts and McCoid, 1991), the Northern Mariana Islands (Crampton, 1921; R.P. Owen, 1974; Wiles et al., 1990), Marshall Islands (Fulbeck, 1947), and the Federated States of Micronesia (Uchida, 1966, 1967, 1969). The same species is reported to reduce native populations of coconut crabs in Micronesia, leading to an additional loss of protein to local villagers (Uchida, 1966, 1969). The related *Varanus niloticus* is reported to attack pets in Florida, United States (T. Campbell, 2005). In none of these instances are economic costs quantified.

The introduction of *Eleutherodactylus coqui* to Hawaii led to the prediction of potential economic effects to the nursery industry, hotel industry, and residential property values because of the noise pollution caused by the frogs' loud calls (Kraus et al., 1999; Kraus and Campbell, 2002). Some of these effects have subsequently been documented. Negative effects of *E. coqui* on residential property values on Hawaii Island alone have been estimated to be 0.16% of total value for houses within 500m of an infestation and 0.12% for houses between 500–800m of an infestation, leading to a potential loss of revenues of almost US\$8 million/year as frogs continue to spread (B.A. Kaiser and Burnett, 2006). Total costs would increase accordingly should the frogs become well established on Maui or Oahu, with their higher property values (B.A. Kaiser and Burnett, 2006). Realtors on Hawaii Island now include declaration of coqui presence in sellers' disclosure statements (Wu, 2005). An alleged failure to make such a declaration has led to the first lawsuit generated by this pest invasion (Dayton, 2007). Since December 2004, Guam has required nursery shipments from Hawaii to be certified as having been treated prior to export with either a 16% citric-acid solution or a 42°C hot-water drench for five minutes (D. Gee, Guam Department Agriculture, personal communication, 2007), treatments known to kill *E. coqui*. As well, plants imported from Hawaii are temporarily quarantined, preference is given to bare-rooted plants, and public education programs have been launched on Guam (Christy et al., 2007a). Some additional cost to Hawaiian nursery growers must follow from these restrictions, but they have not yet been calculated.

Introduced *Bufo marinus* became a significant predator of honey bees (*Apis mellifera*) in Australia and led to economic losses for apiarists and reduction in

crop-pollination services (Goodacre, 1947; Hewitt, 1956; Tyler, 1994). Consequently, the government of Queensland recommended placing hives on collapsible wooden stands to remove them from the reach of toads. C. Lever (2001) estimated the cost of doing this to be AUS\$1 million for stand procurement and replacement every five years; this excludes labor and transportation costs, which are expected to be heavy (Tyler, 1994). Upon advent of the cane toad in their region, aboriginal communities in the Borroloola area changed their ceremonies to request the spirits to return the local food and totem species lost subsequent to the toad invasion (van Dam et al., 2002). This bespeaks a significant, though unquantified, effect of the toads on the local subsistence economy. Similar impacts were predicted to occur to native communities in the Kakadu region subsequent to toad invasion (van Dam et al., 2002). Cane toads also consume large numbers of dung beetles, which were introduced to Australia to rid the continent of accumulating waste from non-native ungulates introduced for ranching (Waterhouse, 1974). Although the costs of this consumption of beetles do not appear to have been calculated, the threat of an upsurge in cattle dung was serious enough to prompt the search for additional dung beetles that would be immune to toad predation (Waterhouse, 1974). These toads have repeatedly been noted to poison naive domesticated pets (e.g., Rabor, 1952; Gebhardt, 1967; Krakauer, 1968; Otani et al., 1969; Roberts et al., 2000), leading to some unmeasured degree of veterinary and replacement costs. Research costs to Australia in an effort to identify a means of controlling cane toads have been estimated at AUS\$500,000/year (Bomford and Hart, 2002) and have totalled more than AUS\$9.5 million as of 2006 (Shine et al., 2006). As well, the Northern Territory has pledged AUS\$100,000/year for a three-year program of research to identify long-term control methods for the species, and Western Australia invested AUS\$600,000 to develop a strategy to prevent toads from entering that state (R. Taylor and Edwards, 2005). Far higher research and mitigation costs are proposed for the future (T. Robinson, 2006).

Green iguanas (*Iguana iguana*) and black spiny-tailed iguanas (*Ctenosaura similis*) have become nuisance problems in southern Florida, eating residential and commercial landscape plantings and digging burrows that can undermine human structures (Krysko et al., 2003a, 2007a). Costs of these activities are unestimated but likely to be significant in aggregate, though widely dispersed.

Information on control and prevention costs for invasive species, including reptiles and amphibians, are rarely made public and are often difficult to obtain. Nonetheless, these costs can be illustrated in a few cases. Control costs (including research and public-outreach expenses) for *Eleutherodactylus coqui* in Hawaii for Fiscal Year (FY) 2007 are in excess of US\$4.2 million, increasing dramatically from approximately US\$1 million in FY 2005 (M. Wilkinson, Hawaii Department of Land & Natural Resources, personal communication, 2007). Costs to control *Rana catesbeiana* in five ponds in Germany has been estimated at € 270,000 annually (Reinhardt et al., 2003). Costs to control the same species for three years in two ponds in England summed to £20,000, excluding personnel time and in-kind costs (Inskip, 2003); costs across seven ponds managed since 1999 have now summed (as of early 2008) to £100,000 (J. Foster, Natural England, personal

communication, 2008). Since 1994, there has been a control program on Guam to prevent brown treesnakes from accidentally being shipped to other localities. Direct programmatic costs for FY 2006 were US\$5.76 million and do not include additional expenses provided by in-kind services (E.W. Campbell, United States Fish & Wildlife Service, personal communication, 2007). During that same fiscal year, the State of Hawaii spent US\$210,000 to inspect vehicles and cargo arriving from Guam to ensure they were free of brown treesnakes (D. Cravalho, Hawaii Department of Agriculture, personal communication, 2007). Total federal funding for the brown treesnake program in FY2007 was US\$6.26 million; this included costs of both operations and research (E.W. Campbell, United States Fish & Wildlife Service, personal communication, 2007).

Control costs for future protection of human health from the alien viper *Protobothrops mucrosquamatus* on Okinawa have been estimated to vary from 430 million to 10.8 billion yen (US\$3.7–93 million) in the first year of operations, depending on how densely traps might be employed for snake control (Nishimura, 2005). To this cost are added depreciation costs varying from 130 million to 2.3 billion yen (US\$1.17–20.6 million) each year. These costs do not include direct economic harm caused by the snakes, such as hospitalization costs, lost agricultural productivity, or lost tourism revenue (Nishimura, 2005).

Health

Brown treesnakes are rear-fanged and venomous and have been responsible for many instances of snakebite on Guam, 80% of which have involved individuals sleeping in their homes (Fritts et al., 1990, 1994; Rodda et al., 1997). A majority of victims seeking or requiring medical treatment have been children less than six years of age (Fritts et al., 1994), and several infants exhibited signs of serious envenomation, including respiratory distress or temporary neurological impairment (Fritts et al., 1990, 1994). The potential of this snake to generate medically serious envenomation in infants is well established. Although fatalities have not been documented, doctors have privately related that they believe some early unexplained child fatalities exhibited the same symptoms later recognized in sublethal envenomations by brown treesnakes (G. Rodda, United States Geological Survey, personal communication, 2008). Thus, it may be that a few human fatalities have occurred from this snake. The odd pattern of biting predominately sleeping humans, biting predominantly small children, and frequent coiling around victims suggests that many bites represent attempted feeding behavior by the snake (Fritts et al., 1994; Rodda et al., 1997; Fritts and McCoid, 1999). Recent figures indicate that approximately 150 brown treesnake bites require emergency-room treatment each year (S. Shwiff, United States Department of Agriculture, personal communication, 2007).

Rear-fanged snakes, such as *B. irregularis*, are generally not as dangerous to humans as the highly venomous front-fanged snakes of the families Elapidae and Viperidae, many of which easily kill adults. The fact that members of these families (*Naja kaouthia*,

Protobothrops elegans, *P. mucrosquamatus*) have successfully established alien populations on Okinawa raises a potentially more serious health issue than is presented by *B. irregularis* in Guam. The two alien vipers of the genus *Protobothrops* are more aggressive than the native *P. flavoviridis*, and *P. elegans* has already been calculated to have a nine-fold greater rate of human envenomations than the native species (Nishimura, 2005). It has been estimated that once the related *P. mucrosquamatus* expands over much of Okinawa in the next century it will cause between 112–258 bite cases annually, much higher than the approximately 60 annual cases caused by its native congener (Nishimura, 2005). Variance in these estimates depends on how far and how fast the alien viper spreads as well as how aggressive it truly proves to be as human-contact frequency increases. Other dangerously venomous snakes have been introduced intentionally or accidentally through the pet trade to numerous other jurisdictions (Appendix A), and their potential to create grave health risks should be obvious.

A similar threat is posed, but not yet realized, by alien populations of large constricting snakes. Pythons (*Python molurus*) are now established in southernmost Florida, and population densities are high and increasing. This species attains a length of at least 7 m, is known to eat leopards in its native range (C.H. Pope, 1935), and can be exceedingly cryptic. Several instances of pythons killing and eating alligators (*Alligator mississippiensis*) in the Everglades are already documented. Although it is unlikely to be a frequent occurrence, it seems fairly likely that a visitor to Everglades National Park or surrounding area will eventually be killed by one. Similar concerns would pertain to other massive snakes (*Python reticulatus*, *P. sebae*, *Eunectes* species) should they become established in Florida or other localities.

Flinders Island spotted fever is a recently recognized human rickettsiosis (R.S. Stewart, 1991). Endemic reptile ticks (*Aponomma hydrosauri*) have been identified as a reservoir, and possibly a vector, of the disease (Stenos et al., 2003; Whitworth et al., 2003). Although the rickettsia, ticks, and reptile hosts are all native to the system studied, the potential for a reptile-borne tick to vector a human disease is newly recognized and raises the possibility that other, currently unrecognized, human diseases may accompany the widespread dispersal of reptile ticks via the pet trade. This may be particularly obvious in the case of the African tick *Amblyomma variegatum*, sometimes vectored by *Varanus* lizards, and known to carry the human disease agent *Rickettsia africae* (Burrige, 2001). An outbreak of human Q fever was associated with the handling and removal of alien ticks from imported reptiles and is suggestive of a possible connection between the two, but direct evidence for a causal relationship remains lacking (Burrige et al., 2000a; Burrige, 2001).

Alien frogs (*Eleutherodactylus johnstonei*) and toads (*Bufo marinus*) in Barbados have been reported to host serovars of *Leptospira interrogans* that are pathogenic in humans, livestock, and domestic dogs (Everard et al., 1988, 1990). Everard et al. (1990) argued that amphibians may be more involved in human leptospirosis epidemiology than currently appreciated, but this supposition remains uninvestigated. Similarly, it has been noted that cane toads can carry extremely high levels of pathogenic *Salmonella* and related bacteria (O'Shea et al., 1990; Thomas et al., 2001), as well as pathogenic *Leptospira* (Babudieri et al., 1973; Everard et al., 1980, 1983, 1988), but it is unknown whether wild populations of this species have

a practical role in causing disease for humans. In Guam, it has been determined that *Bufo marinus*, *Anolis carolinensis*, and *Carlia ailanpalai* have high infection rates for *Salmonella* species, including *S. waycross*, a serotype that contributes significantly to high human salmonellosis rates in Guam but is rare in other countries (Haddock et al., 1990). High prevalence of *Salmonella* in fenced yards that exclude feral mammals has led to the inference that these lizards and toad are significant contributors to the high prevalence of salmonellosis in Guam (Haddock et al., 1993). In the United States, 6% of all *Salmonella* infections (and 11% of those in patients <21 years of age) are related to contact with amphibians or reptiles, which equates to approximately 74,000 cases/year (Mermin et al., 2004). Exposure in these cases is attributable to keeping reptiles and amphibians as pets and not to established populations of alien species per se. However, this finding does show the potential for similar transmission via close contact with alien species – such as house geckos and Cuban treefrogs – that are commensal with humans in the tropics and commonly reside and defecate in homes or cisterns. As far as I know, disease transmission via these routes has not been examined; however, health officials in the British Virgin Islands attempt some control of Cuban treefrogs because of their propensity to occupy cisterns used for collecting residential water (Owen et al., 2006).

Cane toads serve as a mechanical vector for human helminths in its native range (Marinkelle and Willems, 1964) and in Puerto Rico (Hoffman and Janer, 1941) because of its coprophagous habits. Hence, they have been conjectured to serve as vectors for human diseases or helminth parasites in areas lacking proper sanitation (Hoffman and Janer, 1941; Freeland, 1985; van Dam et al., 2002). However, the epidemiological importance of these conjectures in any portion of its introduced range remains unexamined.

There is one documented case of human death following ingestion of three cane toads that were mistaken for an edible species (Rabor, 1952). This species has also been reported to cause illness in humans after handling (Allen and Neill, 1956; Gebhardt, 1967) and after toxin entered open scratches (Gebhardt, 1967; Otani et al., 1969). Contamination of water sources by dead *Bufo marinus* has been reported for Palau (Gressitt, 1952) and Australia (van Dam et al., 2002). In at least the former instance, contamination threatened scarce water resources on an atoll. The threat is created by the sometimes large numbers of toads that may die and rot in a water source, as well as their released toxins, which may possibly be stable in such an environment for several days (van Dam et al., 2002).

Tadpoles of *Bufo marinus* have been shown to have a depressive effect upon growth rates in four species of mosquito and on survival rate in one species when reared together in small containers of water (Hagman and Shine, 2007). Although many variables remain unresolved (e.g., cane toad effects on native anurans and native mosquito predators, fitness of different size classes of mosquitoes), this has led to the speculation that cane toads might potentially have a suppressive effect on mosquito populations in the wild and lead to reduced transmission rates of mosquito-vectored diseases for humans (Hagman and Shine, 2007).

Green iguanas (*Iguana iguana*) have become abundant on Puerto Rico, where they now pose an airstrike hazard at San Juan's international airport (Engeman et al., 2005b). There have been five collisions of airplanes with iguanas at this location, and flight operations were temporarily halted six times during a two-month period in 2001 because of iguana incursions on the runways (Engeman et al., 2005b). The size and abundance of these lizards make them an important airstrike hazard in San Juan and of potential importance at airports in other parts of their introduced range (Engeman et al., 2005b).

Scientific Loss

The irreversible damage that alien invasions can cause is not limited to ecological and economic impacts but includes epistemological loss as well. Information lost can include knowledge of original range for a species, evolutionary status of populations, and ecological relationships within invaded regions. Such knowledge loss can have practical importance for conservation efforts.

Rampant introduction of reptile and amphibian species has resulted in many species being cryptogenic; that is, the distinction between their native vs. introduced ranges is obscure or totally unknown (Carlton, 1996). The term was originally coined in the context of marine species, many of which have presumably hitchhiked on the bottoms of ships for thousands of years, resulting in complete uncertainty about the extent of their original ranges. However, among reptiles and amphibians many examples exist too, and most are derived from introductions made prior to the historically recent period of scientific documentation. It is almost certain that the set of lizards (*Gehyra mutilata*, *G. oceanica*, *Hemidactylus garnotii*, *Hemiphyllodactylus typus*, *Lepidodactylus lugubris*, *Nactus pelagicus*, *Cryptoblepharus poecilopleurus*, *Emoia cyanura*, *E. impar*, *Lipinia noctua*) that occurs throughout most of the Pacific islands has been introduced by humans through at least part of this region during the past two millennia. However, we do not yet know in most cases exactly where they were introduced; we know in none of these cases where exactly their native ranges lie. To discriminate among the two, detailed molecular studies using a variety of sensitive markers and comprehensive geographical sampling need to be done; to date, these are lacking. So, it remains virtually certain that much of the currently occupied ranges of these species are due to human introductions (e.g., Moritz, 1987; Beckon, 1992; Moritz et al., 1993; Fisher, 1997; Austin, 1999; Ineich, 1999), but details are opaque.

Identical problems hold in many other regions. In the Caribbean, which islands were occupied by *Eleutherodactylus johnstonei*, *E. martinicensis*, *Geochelone carbonaria*, and *Iguana iguana* prior to human activities are variously argued about but not known with confidence (Underwood, 1962; Lazell, 1973; Lescure, 1983; Censky, 1988; Corke, 1992; H. Kaiser, 1992, 1997; Breuil, 2002; Powell, 2004). It is uncertain whether the population of *Trachemys decussata* on Grand Cayman is native or introduced by Amerindians (Seidel, 1996). In France, the native range of

Rana ridibunda is obfuscated by recent introductions of allochthonous frogs (Pagano et al., 2003). Paleontological (Alcover and Mayol, 1981) and some biochemical evidence (Hemmer and Kadel, 1980; Hemmer et al., 1981) suggests that few species of reptiles and amphibians occurred on the Balearic Islands until human occupancy and that most of the current herpetofauna there is introduced. Similar results may obtain elsewhere on Mediterranean islands (e.g., Böhme and Wiedl, 1994; Corti et al., 1999; Pascal et al., 2006; but see Vigne et al., 1997 for a counter-example) but have not yet been conclusively demonstrated. In Madagascar, the few species shared with mainland Africa have sometimes been suspected to be introductions; for example, *Kinixys belliana* is argued to be an ancient introduction (Bour, 1978, 1987, 2006). However, Madagascan *Ptychadena mascareniensis* – another species shared with mainland Africa – has recently been shown to be native (Vences et al., 2004a), and *Kinixys* merits similar testing. The lizard *Zonosaurus madagascariensis* on Aldabra and Curieuse in the Seychelles is variously argued to be introduced (Henkel and Schmidt, 1995) or native (Matyot, 2003). The parthenogenetic blind snake *Ramphotyphlops braminus* now has a virtually pan-tropical distribution, most likely having travelled with humans for millenia. It's origin is unknown but is likely to be southern Asia, where its presumed closest relatives live (A. Wynn, United States National Museum, personal communication, 2006).

Conversely, the obvious fact that herpetological species are transported by humans has led to a number of uncritical claims for human introduction that have no direct or compelling inferential evidence. For example, C. Lever (2003) asserted without evidence that a variety of lizards native to islands of the central Pacific are alien (see Appendix B). Brown and Alcalá (1970) provided a list of 23 reptiles and amphibians that they asserted were non-native to the Philippines, and Iskandar and Tjan (1996) did the same for 19 species of reptiles and amphibians on Sulawesi, an assertion repeated by Inger and Voris (2001). But these claims were based solely on distributional evidence and ability to thrive in human-disturbed habitats (Brown and Alcalá) or distributional impressions on an imperfectly studied island (Iskandar and Tjan). In the latter case, the authors acknowledged that some of their records could be nothing more than cases of mistaken provenance. Prior belief that the endemic *Indotestudo forstenii* of Sulawesi was also a human introduction (Pritchard, 1979; Groombridge, 1982; Hoogmoed and Crumly, 1984; Iskandar, 2000) has been shown to be false (Iverson et al., 2001), so such assertions should be viewed (and made) with caution. Nonetheless, these claims, though not yet compelling, do highlight the potentially significant complement of cryptogenic species within a wide array of insular herpetofaunas. Some of these hypotheses of human-mediated origins are potentially testable by investigation of patterns of genetic variation, but that need not always be the case, and some cryptogenic species will undoubtedly remain lost to scientific understanding.

Taxonomic clarity too can suffer from alien reptile introductions, as indicated by the case of *Anolis distichus* in Florida discussed earlier. In that instance, taxonomic distinctiveness of a possibly native lineage was obliterated by genetic introgression of foreign genomes, and it is now likely impossible to determine whether *A. d. floridanus* was truly a native Floridian element or an older introduction. Turtles provide

equally instructive examples. Bahaman turtles of the genus *Trachemys* have apparently not been native members of the fauna of the Great Bahama Bank in recent times but may have been in the Pleistocene (Seidel, 1988, 1996). Until recently, turtles from Cat Island and Eleuthera on this bank have been treated as an endemic species and considered highly endangered (Groombridge, 1982). More recently, they have been shown to be conspecific with the Jamaican species *T. terrapin* and are presumed to be introduced (Seidel and Adkins, 1987; Seidel, 1988). However, Lee and Ross (2001) argue alternatively that *T. terrapin* is native to the Great Bahama Bank and prehistorically introduced to Jamaica. Taxonomic confusion about Caribbean *Trachemys* persisted for many years because morphological variability within the genus had been difficult to assess. This was worsened in the Bahamas by introduced *Trachemys* species creating hybrid swarms, resulting in additional phenotypic confusion (D.G. Campbell, 1978; Groombridge, 1982; Seidel and Adkins, 1987; Seidel, 1988). Foreign *Trachemys* species introduced to the Bahamas include *T. stejnegeri* (Seidel, 1988), *T. terrapin* (Seidel, 1988), *T. decussata* (Lee, 2004), and *T. scripta* (Lee and Ross, 2001; Mealey et al., 2002; Lee, 2004), and some of these introductions continue to be made (Mealey et al., 2002; Lee, 2004). Because of this history of human intervention, taxonomic resolution of Bahaman *Trachemys* was delayed until populations on the Great Bahama Bank were very small. The result is that, without clearer historical resolution of directionality of movement for *T. terrapin*, it remains uncertain whether Bahaman populations are endangered native elements or foreign interlopers, although the latter presently seems more likely.

Similar problems plague understanding of the giant tortoises of the granitic Seychelles. It is clear that one or more species of tortoise was native to these islands inasmuch as they were noted to be common when the islands were discovered (Stoddart and Peake, 1979). However, these original populations were exterminated, and tortoises from Aldabra were later imported in large numbers. Modern giant tortoises from the granitic Seychelles can have a diversity of shapes (Bour, 1984c), which has led some to treat them as separate species (Gerlach and Canning, 1998), but molecular evidence shows them to be identical or virtually identical to each other and to Aldabran tortoises (Austin et al., 2003; Palkovacs et al., 2003; Karanth et al., 2005). In the absence of DNA evidence from subfossil specimens that unequivocally pre-date human settlement, it remains unknown whether the species that is now restricted to Aldabra naturally occupied the granitic islands or whether those islands contained only extinct endemic species. So, it remains uncertain whether the numerous introductions of Aldabran tortoises to the granitic Seychelles represent instances of reintroduction of a native species or introduction of an alien, although I have conservatively treated them herein as the latter.

It is clear from these examples that loss or muddling of taxonomic or distributional knowledge can have practical ramifications for conservation above and beyond merely reducing the total fund of human knowledge. Another example is provided by the pool frog, *Rana lessonae*, known to be introduced into Great Britain several times since the mid-1700s. It has long been thought that all populations within Great Britain originated from such introductions, but recent evidence

has confirmed that a few populations (now all extinct) were native and unrelated to the lineages from which introduced animals were descended (Gleed-Owen, 2000; Zeisset and Beebee, 2001; Wycherly et al., 2002; Beebee et al., 2005; Snell et al., 2005). Without the introductions, the species would likely have been recognized as a native element of the British fauna sooner, perhaps in time to prevent its extirpation there. Similar problems hold in the case of *Iguana iguana* and *I. delicatissima*. The former is widespread across tropical America and parts of the Lesser Antilles; the latter is endemic to some of the Lesser Antilles. The native range of *I. iguana* in the Antilles is uncertain, but some populations are certainly introduced (Lazell, 1973; Lescure, 1983; Breuil, 2002). On Guadeloupe and the adjacent Îles des Saintes, the two species have been hybridizing, with *I. delicatissima* populations disappearing in the process (Day and Thorpe, 1996; Day et al., 2000; Breuil, 2000a, b, 2002). Clearer knowledge of the native range of *I. iguana* might have generated concern for a possible introduction and instigated mitigative measures to avert this loss, but such data were and remain lacking.

Other scientific losses occasioned by herpetological introductions are widely recognized, even as they remain largely undiscussed. Primary among these is that the original ecological dynamics in unique regions or habitats heavily invaded by alien reptiles and amphibians are likely to never be understood. The cascade of effects attendant upon introduction of *Boiga irregularis* to Guam (Fritts and Rodda, 1998) well illustrates the loss of understanding of original ecological dynamics that can occur subsequent to an invasion. Similar epistemological effects certainly apply to regions already heavily invaded by alien reptiles and amphibians, such as southern Florida, Hawaii, and Okinawa, and they likely occur even in areas having only a single significant herpetological introduction, such as the Ogasawara Islands. It is reasonable to expect this loss of scientific knowledge to be common even though it typically goes unremarked. In a broader sense, because much of ecology involves understanding spatial and temporal scales of disturbance regimes and the ecological patterns thereby derived, when an area becomes overwhelmed by alien introductions, the ecological dynamics and patterns due to other disturbance regimes are liable to be masked and less accessible to understanding. These problems, of course, are compounded in places like Hawaii or the Mascarene Islands where massive introduction regimes are superimposed upon large numbers of native-species extinctions.

One final epistemological loss extends far beyond the realm of science and its application. It is widely noted that modern humans are becoming increasingly alienated from nature, concomitant with increased concentration of human populations in urban areas far from any sustained contact with nature. This alienation can make it difficult to gain public acceptance for biologically sensible conservation-management decisions because large segments of society are cognitively divorced from the biological realities upon which their lives are based. One way in which this problem is worsened is by introduction of alien species, which, because of their frequent abundance, will often be unthinkingly accepted by most people as “normal”, implicitly interpreted to mean “native”. This has practical implications for native plants and wildlife by making needed control of invasive aliens harder for an

uninformed public to accept, sometimes leading to unnecessary opposition to alien-species control programs needed to prevent extinctions of native species. I am unaware of any studies to quantify the effects of this particular form of social ignorance upon policy or managerial decisions, but the impression for many actively involved in management of invasive species is that it often leads to significant problems.

Conclusions

As the survey above indicates, a wide variety of negative impacts has been shown to attend the introduction of alien reptiles and amphibians – impacts that mirror many of those seen in better-studied groups like mammals. Despite this diversity, it is important to note that only a small subset of naturalized species or populations has received any form of impact study. Hence, while at least 322 species of reptiles and amphibians have been naturalized across the globe, only 14 species have had ecological impacts demonstrated or reasonably inferred (Table 3.2). Of these, only three species (*Boiga irregularis*, *Bufo marinus*, and *Rana catesbeiana*) could be said to be even moderately well studied; most of the remainder have had impacts demonstrated in only one or a few studies of limited scope. Similarly, evolutionary impacts have been demonstrated or implied for 17 species. Most of these involve instances of hybridization with native relatives. Although not all instances of hybridization have been demonstrated to have importance at the population level, several clearly do. Lastly, economic or health impacts on humans have been demonstrated ($n = 4$) or implied but not compellingly proven ($n = 2$) for six species. In total, excluding instances of epistemological loss of knowledge, which are currently too numerous and uncertain to quantify, 26 species of reptiles and amphibians are demonstrated to have caused or are credibly implicated in ecological, evolutionary, economic, or health effects on native wildlife or humans (Table 3.2).

It could be argued that this small number reflects the fact that alien reptiles and amphibians are largely innocuous and warrant ignoring. That is possible, but it is neither a scientifically cautious nor compelling interpretation. More likely, this modest number reflects widespread inattention to impact phenomena among reptiles and amphibians and the difficulty of convincingly demonstrating them. Consistent with that interpretation is that the large majority of articles cited above have been published in the past 20 years and that such studies are dramatically increasing in frequency (Fig. 3.1). Most of the earlier studies recorded in Fig. 3.1 are merely anecdotal references; experimental studies didn't begin until the 1970s. Further, the species demonstrably or likely causing impacts for which dates of introduction can be estimated (this excludes several more ancient introductions of undetermined age) were introduced from 20–175 years ago, with an average introduction date of 62 years ago. Since approximately two-thirds of all herpetofaunal introductions have occurred in the past 60 years, the lag in scientific study alone suggests that a considerably larger pool of impacts will eventually emerge. This

Table 3.2 Impacts reported for alien reptiles and amphibians, excluding species reported to affect only other aliens. Only a few examples of taxa involved in loss of scientific understanding are listed because of the large and uncertain size of this cohort

Impact	Species
Ecological	
Predation	<i>Anolis carolinensis</i> , <i>Anolis sagrei</i> , <i>Boiga irregularis</i> , <i>Bufo marinus</i> , <i>Natrix maura</i> , <i>Osteopilus septentrionalis</i> , <i>Rana catesbeiana</i> , <i>Xenopus laevis</i>
Poisoning	<i>Bufo marinus</i>
Secondary trophic effects	<i>Anolis carolinensis</i> , <i>Boiga irregularis</i> , <i>Bufo marinus</i> , <i>Carlia ailanpilai</i> , <i>Hemidactylus frenatus</i> , <i>Rana perezii</i>
Competition	<i>Anolis carolinensis</i> , <i>Anolis sagrei</i> , <i>Bufo marinus</i> , <i>Carlia ailanpilai</i> , <i>Eleutherodactylus johnstonei</i> , <i>Hemidactylus frenatus</i> , <i>Osteopilus septentrionalis</i> , <i>Podarcis sicula</i> , <i>Rana catesbeiana</i> , <i>Trachemys scripta</i>
Disease vector	<i>Ambystom tigrinum</i> , <i>Rana catesbeiana</i> , <i>Xenopus laevis</i>
Evolutionary	
Hybridization	<i>Ambystom tigrinum</i> , <i>Anolis distichus</i> , <i>Anolis sagrei</i> , <i>Cuora flavomarginata</i> , <i>Emys orbicularis</i> , <i>Iguana iguana</i> , <i>Podarcis sicula</i> , <i>Protobothrops elegans</i> , <i>Rana esculenta</i> , <i>Rana lessonae</i> , <i>Rana ridibunda</i> , <i>Sauromalus spp.</i> , <i>Trachemys scripta</i> , <i>Triturus carnifex</i>
Changed morphology	<i>Bufo marinus</i>
Changed physiology	<i>Bufo marinus</i>
Changed behavior	<i>Bufo marinus</i> , <i>Natrix maura</i> , <i>Rana catesbeiana</i>
Economic	
Agriculture	<i>Boiga irregularis</i> , <i>Bufo marinus</i> , <i>Varanus indicus</i>
Power supplies	<i>Boiga irregularis</i>
Property values	<i>Eleutherodactylus coqui</i>
Human Health	
Envenomation	<i>Boiga irregularis</i>
Water contamination	<i>Bufo marinus</i>
Disease vector	<i>Bufo marinus</i> , <i>Eleutherodactylus johnstonei</i>
Airstrike hazard	<i>Iguana iguana</i>
Scientific	
Biogeography	<i>Cryptoblepharus poecilopleurus</i> , <i>Eleutherodactylus johnstonei</i> , <i>Eleutherodactylus martinicensis</i> , <i>Emoia cyanura</i> , <i>Emoia impar</i> , <i>Gehyra mutilata</i> , <i>Gehyra oceanica</i> , <i>Geochelone carbonaria</i> , <i>Hemidactylus garnotii</i> , <i>Hemiphyllodactylus typus</i> , <i>Iguana iguana</i> , <i>Lepidodactylus lugubris</i> , <i>Lipinia noctua</i> , <i>Nactus pelagicus</i> , <i>Rana ridibunda</i> , <i>Trachemys decussata</i>
Taxonomy	<i>Anolis distichus</i> , <i>Trachemys spp.</i>
Ecology	<i>Boiga irregularis</i>

will be even truer if lag phenomena among the naturalized populations themselves should prove common. So it seems likely that instances of ecological, evolutionary, health, and economic impacts from herpetological introductions will multiply as additional alien populations expand and become studied. This is further suggested

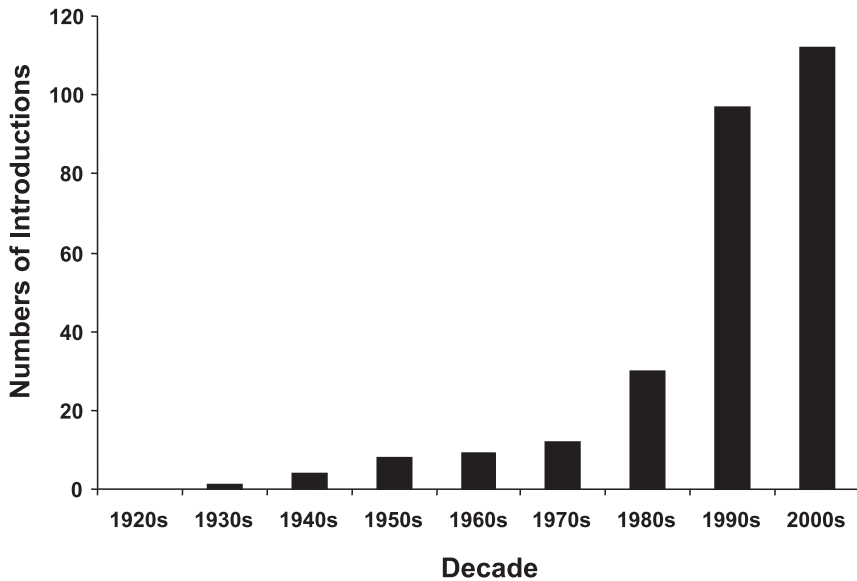


Fig. 3.1 Growth in number of scientific studies that treat the ecological and evolutionary impacts of alien reptiles and amphibians

by the large number of literature claims not surveyed here that purport, but do not document, the decline of native species of herpetofauna coincident with the advent of alien forms.

The late genesis of these impact studies is problematic in another way. The absence of such studies seems sometimes to have been interpreted as demonstrating the absence of impacts, especially when combined with the absence of obvious effects upon casual inspection – effects that we’ve grown to expect to be obvious because they are apparent for many plant, mammal, insect, or forest-pathogen invasions. The problem is that impacts caused by invasive herpetofauna are usually not obvious, even to trained biologists. Instead, they have proven to be subtle and difficult to discern without careful study. This form of denial was perhaps most apparent in the case of the brown treesnake – a species now widely viewed as the poster child for invasive herpetofauna, but which was vehemently denied as having any role in Guam’s bird declines until years of careful research (Savidge, 1987a; Savidge et al., 1992) demonstrated that position to be baseless. But earlier claims for the neutral effect of Florida’s alien herpetofauna (L.D. Wilson and Porras, 1983; Butterfield et al., 1997) – claims repeated for other jurisdictions too (e.g., McKeown, 1996) – also seem to reflect this pattern of reasoning. In raising this issue, I in no way intend to argue that most herpetological introductions do or will impose damaging impacts. I simply don’t know whether that’s true or not; insufficient data have been gathered to allow for generalizations. But I will argue that the diversity of evidence provided above shows herpetological invasions cause or are likely to cause far more damage than they have hitherto been credited with. Moreover, I suggest this

evidence is sufficient to justify a precautionary approach with respect to further herpetological introductions, thereby meriting the devotion of greater management attention to this phenomenon. I proceed from this conclusion to now inquire what management actions have been taken in response to these invasions.

Chapter 4

Management Responses

Management actions against invasive herpetofauna have slowly increased as awareness of their impacts has advanced, although management has not yet progressed to the level of routine success that frequently characterizes actions against invasive mammals or plants. Logically, alien herpetofaunal management may occur at any of the three stages of the invasion process discussed in Chapter 1: preventing introductions from occurring, establishing early-detection and rapid-response programs to eradicate incipient populations, or managing well-established pests long-term so as to mitigate their worst effects. As for other alien species, impact reduction will most effectively be achieved by having a strong prevention program to keep herpetofauna from travelling and naturalizing outside their native ranges. To create such a program involves knowing the details of how species are transported by humans, and research requirements to meet that need will be examined in the next chapter. However, prevention programs can never be perfect barriers to introduction, so it also remains important to determine to what extent eradication and long-term control programs may prove effective against naturalized herpetofaunal populations. Relatively few attempts have been made in this direction, and they are not widely publicized, but I review here the instances of which I am aware.

Prevention

Before considering eradication and control programs, let us briefly review the range of prevention options that have been adopted against alien reptiles and amphibians. By and large, such efforts have been sparse. Most governmental jurisdictions do not approach import restrictions on reptiles and amphibians in any sort of comprehensive or coordinated manner. Instead, if they act at all, governments typically ban a few species known or believed to be pests, and restrictions may be independently adopted by a variety of agencies. In the case of the United States, for example, the Fish and Wildlife Service prohibits only the brown treesnake from import without a permit (U.S. Code of Federal Regulations: Title 50 CFR Section 16.11–16.15); the Department of Agriculture prohibits three tortoise species (*Geochelone pardalis*, *G. sulcata*, and *Kinixys belliana*) because they are known carriers of African ticks

that serve as vectors for heartwater disease (U.S. Code of Federal Regulations: Title 9 CFR Sections 74.1, 93.701); and public health regulations prohibit the importation of turtles smaller than four inches, or their eggs (Title 42 CFR Section 71.52–53). Each of these restrictions was imposed in reaction to widespread publicity of one-time newly identified, specific threats: extinction of birds on Guam caused by brown treesnakes, potential for importation of heartwater disease via tick-infested tortoises, and *Salmonella* transfer between young turtles and children, respectively. In a somewhat more proactive vein, in 2000, the United States Fish and Wildlife Service solicited risk analyses for a variety of species it identified as potentially invasive. Taxa were apparently chosen for study based primarily on high commercial trade volume, and two of these studies concerned reptiles or amphibians. Rolan (2003) assessed potential risk of 24 amphibians; Reed (2005) assessed the risk of large boas and pythons and made a series of recommendations to reduce risk from these imports. It is unclear that either report has led to consideration of any regulatory action by the United States Government, but the Fish and Wildlife Service for the past five years has been considering banning the importation of all species of *Boiga*, and that same agency has recently proposed banning the importation of some large constrictors. Other than this one-time effort, coordinated, proactive assessment of invasion risk posed by other species of reptiles and amphibians has not been pursued by the United States.

A similarly taxonomically limited, reactive approach led the European Union in 1997 to ban importation of *Trachemys scripta* and *Rana catesbeiana* (Detaint and Coïc, 2006; Dupré et al., 2006; Scalera, 2007b), although possession of these species is not banned, and both may still be traded among European Union member states (Scalera, 2004). This import prohibition followed widespread naturalization of the two species in climatically acceptable regions of the continent, which generated concern about the potential risks of these notorious invaders to native wildlife. Although some animals continue to be smuggled into some European Union states, arrests aiming to curtail this activity have occasionally been made, and tens of thousands of animals have been seized (Fiore and Avanzo, 2002; Dupré et al., 2006). This ban was followed in 2005 by an additional ban on *Chrysemys picta*, whose importation volume increased dramatically with the curtailment of trade in *T. scripta* (Scalera, 2007b). However, as Scalera (2007b) pointed out, a coordinated effort in the European Union to address invasive species of any kind has not been made, so actions currently are restricted to isolated activities by member states. Genovesi and Scalera (2007) have proposed the adoption by the European Union of a coordinated system of lists covering taxa approved, prohibited, or requiring further study for importation. Doing so would make prevention programs for alien herpetofauna in the European Union far more proactive and effective than the current approach and move it considerably beyond the reactive paradigm adopted by the United States. National prohibitions by European Union member states against alien species are as hit-or-miss as those of the United States, and few of these include mention of reptiles or amphibians (de Groot and Gerrits, 2002).

Guam too has responded to the threat posed by a single herpetological species – in this case the coqui, *Eleutherodactylus coqui*. As noted in the preceding chapter,

Guam Department of Agriculture now requires nursery shipments from Hawaii to be treated prior to export, so as to kill any hitch-hiking frogs, and to be temporarily quarantined upon arrival in Guam. As seen for the United States, there appear to be no broader assessments of herpetological risks to Guam or to the European Union.

More comprehensive or systematic import restrictions against herpetofauna apply in only a few jurisdictions known to me. For example, New Zealand prohibits importation of animals for which they have not established an explicit import policy. Reptiles and amphibians lack such policies; hence, they are prohibited by default. Australia has similar laws, banning the importation of all reptiles and amphibians except for permitted scientific and educational uses. Taiwan also bans the importation of reptiles as pets. Hawaii lies somewhere between the extremes presented by the United States and the austral nations: it allows importation of a set of several dozen species that are approved for commercial sale, it permits several dozen additional species for use by scientific and educational institutions, and it bans all remaining species. In this instance, there is no clear scientific rationale or objective decision-making process for determining which species are included on which list, but there is at least the general application of a precautionary approach. Both New Zealand and Hawaii have explicit legislative prohibition of snake imports, reflecting recognition gained from the brown treesnake of the danger these animals can pose to island faunas. These are the only jurisdictions of which I am aware that take a more general precautionary approach to alien reptiles and amphibians, although I acknowledge that there may well be other examples elsewhere of which I am unaware. My intent is not to present a comprehensive review of importation restrictions but merely to show the range of options available and to illustrate the fact that explicit preventive attention to alien reptiles and amphibians is rare. This poor preventive response can not be viewed as surprising inasmuch as the impacts attending herpetological invasions are not yet widely appreciated, even among invasion biologists. Such ignorance makes import restrictions politically infeasible in most jurisdictions. That Australia, New Zealand, and Hawaii have escaped that bind no doubt reflects heightened sensitivity to alien invasions gained by their extensive tragic experiences with them. It seems likely that most other countries have responded even less to the issue than have the United States and European Union.

Eradication

Attempts to rapidly eradicate recent incursions of alien herps have met with little success to date. A few exceptions exist, however. The best-documented case concerns the Australian frog *Limnodynastes dumerilii*, tadpoles of which were privately reared in captivity from an egg mass found in northern New Zealand in 1999. The individual possessing the frogs soon brought his discovery to the attention of biosecurity officials. Within two months of the discovery, officials had surveyed for eggs, tadpoles, and calling adults in all catchments of the mountain

range in which the egg mass was found; all captive animals were destroyed; and all tadpoles and metamorphs captured at the original site were destroyed (Whitaker and Bejakovich, 2000). Extreme rains during the survey period led to flooding that scoured the stream having the original infestation. All uncaptured tadpoles appear to have been destroyed by that event and no further animals have been found subsequently. Hence, the eradication effort, undertaken at a very early stage of incursion, has been declared a success.

I have been able to find only a few other claims for (relatively) rapid eradication of newly established reptiles or amphibians. The first is the statement by Ota et al. (2004a) that *Bufo gargarizans*, introduced to a site in northern Okinawa, was eradicated from that site (and, by implication, from the island) by a private effort extending from the late 1980s through the mid 1990s. This project involved removal of adults, eggs, and tadpoles, but details on the adopted methodologies were not provided.

The second involves bullfrogs, *Rana catesbeiana*, first noticed at a couple of adjacent ponds in East Sussex, England in 1996. By 1999, hundreds of tadpoles were evident, and an eradication project was begun. This involved survey of 53 ponds and fencing of the 7 found to be infested. Within these ponds, frogs were removed by use of aquatic traps, pit-fall traps, hand-capture, shooting, and electrofishing (Banks et al., 2000; J. Foster, Natural England, personal communication, 2008). At the end of 1999, the ponds were drained so as to exterminate remaining tadpoles, allow surviving frogs to be located and captured, and allow the pond silt to be excavated and buried under compact soil. After several years of effort, this operation netted a total of almost 12,000 bullfrogs, and eradication of these populations appeared successful (Fisher and Garner, 2007). However, bullfrogs have recently appeared at another locality in Great Britain (R. Trout, Forest Research, personal communication, 2007), control of this population is ongoing (J. Foster, Natural England, personal communication, 2008), so complete eradication from the island is not yet assured, though is seemingly feasible.

Similarly, several populations of bullfrogs have been eradicated from Germany. One population was eradicated from Celle, Germany, partly by means of hunting with shotguns (C.R. Boettger, 1941), and a second population near Böblingen exterminated partly by means of electrofishing for tadpoles and by pond fencing (Laufer and Waitzmann, 2002; Veenvliet and Veenvliet, 2002; Ficetola et al., 2007b). Another pond in Meckenheim was fenced and drained, and animals removed (Veenvliet and Veenvliet, 2002), again resulting in eradication (Ficetola et al., 2007b). A fourth population was exterminated from Kiel by freezing weather (Veenvliet and Veenvliet, 2002). Eradication of the same species from a pond in the Netherlands was achieved by capturing tadpoles (Veenvliet and Veenvliet, 2002).

Lastly, three isolated populations of *Xenopus laevis* appear to have been successfully eradicated in the United States. The first population was poisoned; the second inhabited ponds at a fish hatchery, which were drained one autumn so that all animals froze over the winter; the third was removed by trapping and may have been assisted by severe freezing weather (Tinsley and McCoid, 1996).

Islands may sometimes be able to achieve eradication and avoid reinfestation even if the larger jurisdiction to which they belong can not achieve complete, territory-wide eradication. Such could be the case with a pending eradication attempt against *Bufo marinus* on Viwa Island in Fiji. This 60 ha island is one of the last habitats containing the endangered endemic frog *Platymantis vitiana* and the cane toads are thought to present a threat to this species (R. Taylor and Edwards, 2005; Morley et al., 2006). Removal of this species is part of a broader conservation plan for the island that involves the removal of a variety of invasive mammals as well (Morley et al., 2006). Eight ponds on the island have been fenced to exclude toads, thereby preventing their breeding and preventing rehydration of adults during the dry season. Another five ponds have been filled in for the same purpose. To date, the barriers seem to be working, with no tadpoles or metamorphs found within any of the enclosures (C. Morley, University of the South Pacific, personal communication, 2007). Hence, reproduction seems to have been halted. It is intended that future efforts will expand to include removal of adult toads by hand capture and use of traps (Morley et al., 2006). This effort is expected to require 3–4 years to complete, if sufficient funding can be obtained to maintain the program. Because of the small size of the island and the fact that toad reproduction can be prevented without threatening the direct-developing *P. vitiana*, this project is quite promising for local conservation of native wildlife, even though cane toads will remain widespread on other islands in Fiji. However, success is not yet assured because of funding uncertainty.

A similar situation may obtain for coqui, *Eleutherodactylus coqui*, infestations on some islands in Hawaii, although that situation is more complicated and may more correctly be viewed as a long-term management program. These frogs were vectored to, from, and around Hawaii in nursery plants (Kraus et al., 1999; Kraus and Campbell, 2002). Governmental response to the invasion was delayed until well after Hawaii Island became widely and heavily infested (Kraus and Campbell, 2002; Kraus, 2008). Eradication on that island is now unachievable, which is problematic because it holds the major portion of Hawaii's large nursery industry (Kaiser and Burnett, 2006). Consequently, Hawaii Island serves as a source of repeated frog invasions to the other islands of the archipelago and to extra-territorial locations. As a result, populations have become established on Kauai, Maui, and Oahu. Eradication of the few populations known on Kauai and Oahu seems likely to succeed because they were tackled before they became irremediably large. For example, all four established populations on Oahu appear close to being eradicated, with breeding populations now apparently absent and all newly calling animals (newly maturing males that had been silent as juveniles) immediately treated upon first detection. Calling animals have not been heard for many months at any of these sites (S. Williamson, Hawaii Department of Land & Natural Resources, personal communication, 2007). The sole population on Kauai is not far behind and should lack a reproducing population by the end of 2007 (K. Gunderson, Kauai Invasive Species Committee, personal communication, 2007). Programs on both islands involve frequent surveys for calling animals, clearing of thick vegetation to reduce habitat, and frequent spraying with citric acid or hydrated lime to kill frogs. Furthermore, Molokai has successfully avoided infestation due to immediate

prejudiced response to incursions of frogs that appear in infested nursery materials. Success on these three islands was made possible by widespread public awareness of these pests and the negative impacts brought about by their uncontrolled spread on Hawaii Island, coupled with frequent surveys of the sites (nurseries and garden centers of department stores) most likely to receive new incursions. These could be considered additional examples of successful eradication but long-term vigilance against reinfestation from rampant nursery populations on Hawaii Island will be necessary. This is helped by regulatory requirement that all exported shipments from Hawaii Island nurseries known to be infested with frogs be treated with either concentrated citric-acid solution or hot-water spray to kill hitch-hiking frogs. Thus, although successful eradication of coqui populations seems likely to be achieved on Kauai and Oahu, both islands will be faced with long-term management to maintain their expensively acquired coqui-free status.

These examples are among the more successful control operations to date, whether applied across an entire political jurisdiction or just to single islands. More often, control efforts that initially began with the intent to eradicate soon proved that goal to be infeasible because population size was initially underappreciated. Such efforts often seek to couple eradication with the gathering of biological data useful for understanding the invasion. For example, Nile monitors, *Varanus niloticus*, became established in the area around Cape Coral, Florida, in approximately 1990. In 2002, funding amounting to US\$51,000 was obtained to complete what was anticipated to be a one-year eradication program (T. Campbell, University of Tampa, personal communication, 2007). However, in the first month of effort it became obvious that the number of lizards present in the population was far in excess of what could be removed with the time and funds available. Consequently, efforts remained focused on gathering data useful for supporting future control efforts, animals continued to be removed from the population, but eradication was not achieved. This lizard population continues to expand numerically and geographically, but governmental control efforts to follow up on the initial knock-down have not been forthcoming (T. Campbell, University of Tampa, personal communication, 2007).

A virtually identical situation obtains with Burmese pythons, *Python molurus*, in the Everglades region of South Florida. In 2002, a park biologist became concerned with the large and increasing number of sightings of these snakes. There had been 21 sightings prior to 2002 and 27 more in that year alone (Snow et al., 2007b). He consulted outside biologists as to whether an established population might exist and was advised against that concern – even though Dalrymple (1994) had already called attention to remarkably high numbers of large constrictors removed from southern Florida every year. Nonetheless, this biologist continued to collect data on sightings and all retrieved specimens, and he has clearly demonstrated that a python population is thriving in the park and expanding well beyond that domain (Snow et al., 2007b). In 2004, it was hoped that the infestation was sufficiently limited that it might be eradicable; by 2006, it was clear that was not the case. The large numbers of snakes that are obviously present, their extensive range throughout a difficult-to-penetrate terrain, their high reproductive output (up to 100 young/brood), and current lack of effective control methods

render eradication extremely unlikely. Hence, efforts are now focused on identifying effective techniques (mainly trapping) so that long-term control may at least be initiated against what is likely to be a significant environmental pest. This work is made more important by recent work suggesting that this species may survive weather conditions across large portions of the United States (Rodda et al., 2008).

Long-Term Control

Far and away the largest-scale control operation for any alien reptile or amphibian has been the United States' federal program on Guam to keep brown treesnakes from spreading to other Pacific islands. This interdiction program was initiated in 1993, is ongoing, and will likely be needed in perpetuity. Most effort has gone toward (1) reducing snake densities in areas surrounding air- and seaports, so as to decrease their probability of entering cargo and vehicles, and (2) searching outbound cargo and vehicles for hitch-hiking snakes, so as to reduce probability of shipping infested cargo. Population reduction largely depends on employing a dense array of traps to capture snakes, which are then dispatched with prejudice (Engeman and Vice, 2002). Nighttime searches of fences, which tend to be attractive to the snakes as easily traversed highways, also help lower snake numbers (Engeman and Vice, 2001). Cargo searches largely rely on the use of trained dogs (Engeman et al., 1998, 2002), but port workers occasionally find and kill them as well. Reduction of rat populations through use of bait stations also lowers prey populations around ports, increasing the efficacy of snake traps. This program has been responsible for a considerable reduction in the numbers of brown treesnakes leaving Guam and arriving in other jurisdictions, such as Hawaii. Although this program is, strictly speaking, a prevention program designed to protect other islands from infestation by brown treesnakes, it has generated numerous spinoff tools that are directly applicable to control of these snakes on Guam. First, there has been considerable refinement of effective trapping (Rodda et al., 1999d; Engeman and Vice, 2002) and barrier (Perry et al., 1998a; E. Campbell, 1999) methodologies to reduce snake numbers in the geographically restricted areas around the ports and within cargo. These methodologies could be at least partly useful for rapid containment and eradication of brown treesnake incursions elsewhere. Second, considerable work has proceeded on devising attractants (Shivik and Clark, 1999; Shivik et al., 2000; Jojola-Elverum et al., 2001), repellents (Savarie and Bruggers, 1999; Clark and Shivik, 2002), toxicants (Brooks et al., 1998a–c; Savarie and Bruggers, 1999; Savarie et al., 2000, 2001, 2005), and toxicant-delivery systems (Shivik et al., 2002; Savarie and Tope, 2004) to control brown treesnakes at both local- and landscape-level scales (cf. Rodda et al., 1998). Management objectives and applications for each of these tool sets are summarized in detail by E.W. Campbell et al. (1999) and Engeman and Vice (2002). It has been recognized for several years that removal of brown treesnakes from relatively small areas (up to ca. 50 ha) may proceed effectively using existing barrier and trapping

methodologies (Rodda et al., 1999e, 2002). Doing so could be important for short- to medium-term conservation of some of Guam's endangered wildlife; however, for long-term conservation of this biota, control across larger areas is necessary. For control of snake populations across Guam's landscape, work has progressed to the point that a methodology employing large-scale aerial delivery of frozen pinky mice laced with acetaminophen has been evaluated for safety (Johnston et al., 2002) and is being tested for efficacy (Hall et al., 2007). The expectation is that once efficient delivery of large numbers of these baits is better refined, clearance of brown treesnakes from certain landscapes on Guam will allow for re-introduction of endangered native animals to these areas as well as greater security from these pests in port areas. To reach this point has taken over 20 years of research effort and 12+ years of operations effort. Costs of the research and operations programs for brown treesnakes are difficult to obtain, but US\$17.9 million was spent on snake-control operations on Guam from October 2001–September 2007 (M. Pitzler, United States Department of Agriculture/Wildlife Services, personal communication, 2007).

Numerous credible reports and recovered specimens of brown treesnakes have appeared on Saipan, in the Commonwealth of the Northern Mariana Islands, in the past 20 years. However, attempts to recover snakes from these various sightings so as to assess whether an incipient population is established have proven frustratingly difficult. Dissatisfaction with this state of affairs led to the initiation in early 2007 of an intensive three-week trapping and search effort in an area having multiple snake sightings over the past 25 years, so as to determine whether an incipient population could be detected (Hawley and Stanford, 2007). Trapping employed 185 traps, covering approximately 6 ha. Visual and canine searches occurred every night, employing 16–23 searchers/night (J. Stanford, United States Geological Survey, personal communication, 2007). Total effort comprised 5,775 trap nights, 1,660 visual search hours, and 100 canine search hours, with search effort summing to approximately 300 km of forest edge and forest transects; cost for the exercise was approximately US\$89,000 (J. Stanford, United States Geological Survey, personal communication, 2007). Results were negative, although it is uncertain whether this is because an established population is absent or because its members are untrappable because high prey abundance renders traps ineffective. Either way, the scale of effort involved well illustrates what is required to competently assess suspected new incursions of cryptic herpetofauna, even for narrowly circumscribed areas.

Control operations elsewhere have generally been sparse or gone unreported in the scientific literature, but some information can be found in unpublished government reports. Such activities as do occur typically involve attempted removal of a species from a particular, limited area, often in an effort to preserve ecological values for native species in high-quality habitats. Such efforts as I am aware of have fared no better than many of the eradication projects noted above. An early attempt to remove a population of *Caiman crocodilus* in southeastern Florida (Ellis, 1980) appears to have failed (L.D. Wilson and Porras, 1983), and the population is now well established (Meshaka et al., 2004a). Migration from adjacent source areas may have been a contributing factor in this failure. Attempts to remove bullfrogs from a

wildlife refuge in southeastern Arizona met with marginal success (Rosen and Schwalbe, 1996b). Adults and juveniles were targeted by hand-capture, spearing, and use of aquatic traps for several short-duration intervals during the summer months. Although large numbers of frogs were removed each year and mean mass of adults declined through time, frog numbers consistently rebounded between years, suggesting that effort and technology were insufficient to impact the population (Rosen and Schwalbe, 1996b). An attempt to eradicate bullfrogs from nearby Sycamore Canyon, Arizona, is ongoing and, again, involves targeting of adults and tadpoles (Kahrs, 2006). Another effort at bullfrog removal from a site in Washington State resulted in numerous dead bullfrogs but no summary of what effect this effort had on the population (Hays et al., 1999).

In Germany, bullfrogs have inhabited relatively few areas and have been successfully eradicated in at least three locations, as mentioned above. An eradication program involving pond drainage, electrofishing, and netting of adults and tadpoles has also been attempted for the largest series of German populations near Karlsruhe (Veenvliet and Veenvliet, 2002; Reinhardt et al., 2003), but the population persists (Ficetola et al., 2007b). It remains to be seen whether bullfrogs can be eradicated from Germany as a whole or whether long-term control will be required at the larger populations. The potential for bullfrog control or eradication in southwestern France is being assessed through a four-year research and public-education program that began in 2003 (Detaint and Coïc, 2006). In this effort, cover traps and catfish traps have been used to collect adults and tadpoles effectively, but it remains to be seen whether these can be deployed broadly enough to effect eradication of metapopulations, which have spread extensively throughout the region (Ficetola et al., 2007b). Failure to do so will result in constant immigration from nearby populations and re-establishment in treated areas. In Venezuela, local control of bullfrogs has involved shooting adults, spreading lime in water bodies to kill tadpoles, and clearing vegetation (Díaz de Pascual and Chacón Ortiz, 2002). Interest in bullfrog control seems to be growing in a wide variety of locations, judging by the number of websites mentioning this goal. Although many of these initiatives refer to their proposed or ongoing activities as “eradication” operations, they are in fact local control operations that may, if competently executed, result in very localized removal of populations. Complete eradication from jurisdictions may be unlikely except in the few instances, like Britain, that have readily defensible borders, few and small populations, and well-executed control operations. Otherwise, this frog’s reproductive capabilities and the threat of repeated introduction or recolonization from adjacent untreated areas are likely to thwart most “eradication” efforts.

Some of the poor success to date in controlling bullfrogs may be explainable because recent work has shown that population growth rate in bullfrogs is most influenced by tadpole development rate and by early postmetamorphic survival rate (Govindarajulu et al., 2005). Consequently, removal of adults – as most control operations have so far done – may only increase survivorship rates among recent metamorphs by reducing the level of cannibalism they suffer. Modeling suggests that control efforts would better be directed toward removal of recent metamorphs in the autumn months (Govindarajulu et al., 2005), and coupling that effort with

removal of egg masses in the spring may serve as a more effective means of population control. This notion has yet to be field tested.

Control efforts against *Bufo marinus* in Australia have largely been devoted toward public education; research to identify effective means of long-term control; and preventing establishment of new populations on offshore islands, at the southern end of its range in New South Wales, and at the western end of its range in Northern Territory and Western Australia. Much of the border-control activity relies on volunteer labor (R. Taylor and Edwards, 2005; Boulter et al., 2006; Sawyer, 2006).

Attempts at localized removal of populations of *Trachemys scripta* are being made in France (Dupré et al., 2006), but details on operational efforts are lacking. These turtles have been removed from some populations using floating basking traps (Gianaroli et al., 1999), submersible traps (Spinks et al., 2003), and shooting (Mosimann and Cadi, 2004), but these activities were apparently not part of sustained control operations. Eradication of an established population of *T. scripta* in Queensland, Australia is being attempted using traps for basking adults and trained dogs to detect nests (O'Keefe, 2005). Infested ponds have also been filled in and compacted or drained, desilted, and fenced to prevent re-colonization. The success of this project is not yet certain.

Management Limitations

As can be seen from these several examples, prevention and eradication programs against invasive reptiles and amphibians have been sparse. This probably results from the still-common perception that these species do not, by and large, pose sufficient ecological problems that they merit the effort. Just as important, such control operations as have been attempted have met with relatively little success. That result stands in contrast, for example, to the situation for many mammals and plants, where control methods and successful eradication operations are becoming fairly routine (see, e.g., Veitch and Clout, 2002; Nogales et al., 2004; K. Campbell and Donlan, 2005; Howald et al., 2007). There are a variety of reasons, both biological and social, for this poor rate of engagement and success, and these are worth reviewing so as to determine whether and how this currently mediocre record might be improved.

Control operations against alien reptiles and amphibians will very often have to overcome three biological obstacles posed by the alien species themselves: crypsis, high reproductive rates, and high population densities. All three may not be operative in each individual invasion, but they will be for many, and one or two of them are likely to apply in almost all invasions. Crypsis merely refers to the fact that most reptiles and amphibians are difficult to locate. Most species are of small size and get by in life to a large extent by hiding from predators, including land managers and biologists. Even species of moderate or considerable size – such as most snakes – are remarkably effective at hiding. It has been remarked, for example, that one can

stand within a few feet of a large python in Everglades National Park in Florida and not be able to see it. In contradistinction, this problem does not apply to many of the mammals and plants that have been the targets of successful control operations. It does apply to other invasive mammals, such as rats, that have frequently been successfully eradicated, but success in those instances has come only after many years devoted to development of reliable baiting, trapping, and poisoning methods. Even eradication of the larger mammals, such as goats and pigs, has required development or refinement of novel control methodologies over the past few decades. Development of effective control methods may be possible for many alien reptiles and amphibians as well, but those research efforts have barely begun. Methods devised for brown treesnakes, for example, have taken almost two decades of effort and are not yet perfected.

High reproductive rates characterize many herpetological species, including several of the most notorious invasives. Amphibians can often have clutches of hundreds or thousands of eggs, making their intrinsic growth capabilities obvious, but even species with rather small clutch sizes can expand their numbers rapidly. For example, the brown treesnake has a modest clutch size of only 3–12 eggs/brood and 1–2 broods/year (Rodda et al., 1999b; Rodda and Savidge, 2007). Nonetheless, in a favorable environment it was able to march across Guam and largely extinguish its native bird community in slightly less than 40 years. Similarly, the direct-developing coqui can produce perhaps 100–120 eggs/year. By frog standards this is rather modest. Nonetheless, it was able to explode across the landscape of Hawaii Island in less than five years, sometimes increasing from a few calling males to large populations in only six months (Kraus and Campbell, 2002). Many invasive reptiles and amphibians have reproductive capabilities greater than these two notorious invaders, and it seems that intrinsic ability to rapidly establish and expand populations is likely to be a severe constraint to controlling many herpetological invasions.

These high reproductive capacities, coupled with the relatively small size of most herpetofauna, frequently result in populations that occur at high densities. This is especially true for alien populations, which typically escape many of the biotic factors – parasites, predators, and competitors – that may constrain their numbers in their native ranges. To return again to the examples just cited, brown treesnakes have been found to occur at densities on Guam that are the highest known for any terrestrial snake species (Rodda et al., 1999c), attaining 50–100 snakes/ha. Similarly, coqui on Hawaii Island occur at approximately three times the maximum densities attained in their native Puerto Rico, reaching 28,000–89,000 frogs/ha (Woolbright et al., 2006). Such numbers will be daunting for any control operation but are likely to be common for many herpetological invasions. All three of these biological obstacles make it difficult to put all individuals in a targeted population at risk, a precondition for successful eradication operations (Bomford and O'Brien, 1995).

Social obstacles operating among the general public, government officials, and scientists may be no less important in constraining successful control operations but are not often discussed. One or more of four such obstacles are likely to apply to many herpetological invasions: disbelief that either a problem or a solution exists,

positive support for the introduction, opposition to the killing of vertebrates, and lack of appropriate control methodologies. As we saw above, disbelief among biologists that a population was established hindered recognition of the python invasion in the Everglades, and disbelief among government officials that frogs posed a problem was a major factor in the failure to respond in a timely fashion to the coqui invasion in Hawaii (Kraus and Campbell, 2002). Disbelief in the desirability or feasibility of eradication currently appears to be preventing French governmental response to the relatively recent invasion of *Xenopus laevis* (Fouquet and Measey, 2006). Even in the case of brown treesnakes on Guam – among the best documented and studied herpetological invasions – there was widespread dismissal of snakes as the cause of avian disappearance in the early 1980s (J.T. Marshall, 1985; Jaffe, 1994). By the time the snake-predation hypothesis became widely accepted, the birds were gone. To this day it remains easy to hear Guam residents express disbelief that brown treesnakes are a problem, simply because they happen never to encounter the (nocturnal) snakes. My experience is that this type of disbelief remains common among scientists as well, including many specializing in invasive-species research. Disbelief that alien reptiles and amphibians constitute problems or that they merit response is likely to remain widely rooted among the general public, but it is to be hoped that education will increase sensitivity among managers and biologists to the potential severity of herpetological invasions. We are not yet to that goal.

Positive support for herpetological invasions will typically involve only a very small slice of the public, but it has the potential to undermine even determined control efforts widely supported by the general public. Spread of coqui by water-garden clubs and private individuals who liked the sound of the frogs' calls abetted widespread and rapid invasion by that species across Hawaii Island, as did the erroneous belief that the frogs control mosquito and nut-borer populations (Kraus and Campbell, 2002). Many herpetological invasions are initiated as deliberate releases motivated by the desire to have a favorite species living nearby. This is clearly true for *Phelsuma* spp., *Gekko gecko*, and *Chamaeleo jacksonii* releases in Hawaii, and it apparently applies to a number of releases in Florida as well (Wilson and Porras, 1983; Meshaka et al., 2004a). This situation can be made worse if monetary opportunities are provided by the release. The rapid spread of *C. jacksonii* in Hawaii, for example, resulted in large part because numerous individuals wanted to ranch them, establishing populations near their homes from which they could collect animals for sale in the pet trade. Similar pecuniary advantage has been taken of some populations of alien lizards in Florida (Krysko et al., 2003b; Enge and Krysko, 2004; Enge et al., 2004c; T. Campbell, 2005), and it would be unsurprising if this too has led to founding of additional populations there.

Opposition to killing invasive herpetofauna may arise because certain segments of the population oppose the killing of any vertebrate. This was an argument used by a few people opposed to coqui control in Hawaii. Opposition by public "animal-rights" groups had little effect in this instance because exasperation with the frogs' noise was widespread among the public. However, opposition by a government official for the same reason served to hinder response operations for a year or so

and had a far more lasting effect on this invasion. I know of no other instance in which this social factor has yet served as a barrier to herpetological control efforts, but the fact that “animal-rights” groups have even opposed eradication efforts directed against rats (Howald et al., 2005; Towns et al., 2006) suggests that it is only a matter of time before such opposition becomes relevant for other herpetological invasions too. Even without organized opposition to removing alien herpetofauna, area residents often like these animals and oppose their removal (e.g., Enge et al., 2004a). The same can be true for members of the scientific research community (e.g., Holden, 2003).

Control methods effective against invasive reptiles and amphibians, as a group, have been barely researched or applied. As previously noted, considerable research in this direction has been expended against brown treesnakes on Guam. Some of these methodologies are likely to have application against other invasive reptile species, but unmodified transferral is by no means certain and seems unlikely in many cases. For example, traps have proven quite effective at reducing brown tree-snake populations in sensitive port areas on Guam, but those traps are biased toward capturing large animals, trap design took many years of careful research to optimize, and the design is sufficiently particular to brown treesnakes that it cannot automatically be applied against other snake populations, such as pythons or water snakes. Indeed, an attempted application of brown treesnake traps to control *Lycodon aulicus* in the Mascarene Islands failed (Rodda et al., 2002). This is not to suggest that knowledge gained for controlling brown treesnakes is irrelevant to other species, only that additional research will often be required to shape that knowledge to create an effective tool to use against the biological peculiarities of the next focal species. Similarly, identification of concentrated caffeine (Campbell and Kraus, 2002) and citric-acid solutions as effective sprays for killing coqui is likely to have application to some other frog invasions, even though the need for de novo development of these techniques in Hawaii helped delay operations against coqui until such point as total eradication was impossible. Recent work in devising control methods for cane toads has focused on development of traps, attractants, toxins, exclosures, biocontrol, and sterile-male release methods (R. Taylor and Edwards, 2005; Molloy and Henderson, 2006; Schwarzkopf and Alford, 2007). None of these techniques is yet perfected for that species, but should they be, they may prove useful against other anuran invaders as well.

The prospect of using parasites as biological control agents against certain herpetological pests – in particular, brown treesnakes and cane toads – has been considered (e.g., Whittier et al., 1997; Whittier and O’Donoghue, 1998; Holzman, 1999; Telford, 1999; Caudell et al., 2002; T. Robinson et al., 2005) but has not progressed very far. This likely reflects the difficulty of guaranteeing host specificity, vector availability, and demographic significance of biocontrol enemies for most vertebrate species (Howarth, 1999; T. Robinson et al., 2005; Rodda and Savidge, 2007). Indeed, even clinical effects may be lacking in heavily parasitized animals (e.g., Caudell et al., 2002; Jakes et al., 2003), and it remains to be determined to what extent reptile and amphibian populations may be ecologically limited by parasitism. All this makes use of biocontrol against invasive herpetofauna highly

risky, success uncertain, research costs high, and funding difficult to justify (e.g., Colvin et al., 2005). It remains to be seen whether such approaches will ever be relevant to control of reptiles and amphibians, but skepticism is justified.

For most invasive reptile and amphibian species we are in a similar position to where we were in the early 1990s with brown treesnakes or in the late 1990s with coqui – effective control methods have yet to be investigated or even identified. This makes it difficult for managers to respond to reptile and amphibian invasions even when they have the desire to do so. Paucity of management tools is likely to remain a serious roadblock for effective action against invasive reptiles and amphibians for many years to come.

Many of these identified biological and social constraints have been relevant to each of the species against which control operations have so far been attempted (Table 4.1), and this concatenation of constraints has undoubtedly been important in generating the poor record of control success to date. These same limitations will undoubtedly pertain across a wide variety of additional herpetological invasions not yet engaged with. Generally stated, the problem is that the high reproductive rates and high densities formed by many reptiles and amphibians enforce a narrow window of opportunity during which eradication can potentially succeed. Failure to act before this window closes means that most species will rapidly become so dense and widespread that effective action is soon impossible. Running counter to this biologically driven need for a rapid response is the fact that crypsis and the four social constraints – especially entrenched disbelief and undeveloped control

Table 4.1 Constraints operative in control operations already attempted against reptile and amphibian species. + indicates the constraint is operative, – indicates it is not. Number of symbols is my rough estimate of the relative degree to which the constraint applies. Crypsis likely applies to all of these species at one stage of their life cycle or another, but I use the symbols to indicate the degree to which it hinders effective control operations

Species	Constraint						
	Crypsis	High rate of reproduction	High density	Disbelief in problem	Support for invasion	Opposition to killing species	Lack of control methods
<i>Bufo marinus</i>	+	+++	+	–	–	–	–
<i>Bufo gargarizans</i>	+	+++	+	–	–	–	–
<i>Eleutherodactylus coqui</i>	–	+	+	++	+	+	++
<i>Limnodynastes dumerilii</i>	+	+++	?	–	–	–	–
<i>Rana catesbeiana</i>	+	+++	+	–	–	–	+
<i>Varanus niloticus</i>	–	+	–	–	–	–	++
<i>Boiga irregularis</i>	++	–	+	+	–	–	++
<i>Python molurus</i>	++	+	?	+	–	–	++
<i>Trachemys scripta</i>	–	–	–	?	?	?	–

methods – promote delays in recognition and/or response to the invasion, often until after the window of opportunity has closed. That was the exact dynamic operative in the case of coquis in Hawaii, brown treesnakes in Guam, and Burmese pythons in South Florida. That same dynamic was avoided in the cases of *Limnodynastes* in New Zealand and bullfrogs in Great Britain because the threat from each was acknowledged at an early stage and because the limited range and aquatic breeding habits of both species allowed for application of control operations at a narrowly focused spatial scale.

But opportune confluence of the proper social, biological, and temporal factors is unlikely to be fortuitously met for most herpetological invasions, especially until the social limitations of disbelief and undeveloped control methodologies are rectified. Control efforts are likely to be similarly compromised by frequent inability to guarantee long-term investment of funds and personnel in such operations. The odds of successful control can certainly be improved by concerted efforts to remove or neutralize the four social constraints and to pursue herpetofaunal eradications with the same degree of professional planning and resource commitment that now characterize rat and ungulate eradications. Such efforts are feasible and eminently worthy of pursuit, and some means of overcoming those limitations will be discussed in the following chapter. But biological constraints remain likely to prove decisively limiting in many herpetofaunal invasions, and, at least for the foreseeable future, most herpetological introductions once established will prove ineradicable. Hence, I think it is clear that avoidance of further herpetological invasions must rely heavily on well-designed prevention programs. This does not obviate the need for competent rapid-response and eradication programs, but merely recognizes that some invasive reptiles and amphibians will present biological difficulties that do not apply to eradication campaigns against other taxa. Hence, primary reliance on responding to known incursions can never form the foundation of a successful program to stem herpetological invasions. Similar to ensuring personal or public health, prevention of infection is key.

Chapter 5

Implications for Policy and Research

There has been no prior synthesis of pathway information, impacts, or human management of introductions for alien reptiles and amphibians. Yet those data are of critical importance for informing future management and research decisions with respect to these animals. They are especially important inasmuch as the modern flood of invasive species represents one of our greatest conservation challenges. So what general patterns and conclusions emerge from the data provided in the previous chapters?

We have seen that a wide array of pathways has been involved in herpetological introductions, but that six of these have been dominant, even though their importance varies taxonomically, temporally, and geographically. In addition to these, four minor pathways contributed lesser numbers of introductions to the total. We have seen that several of these major and minor pathways revolve around similar, unifying themes: an aesthetic nexus that promotes the keeping of animals and their frequent escape, release, or introduction via private owners, wholesalers, retailers, exhibitors, or zoo personnel, and a trade-goods nexus that transports animals in cargo or vehicles as unintentional hitch-hikers in the course of regional or international trade activities. The patterns of taxonomic, temporal, and geographic variation seen in pathway importance allow scope to investigate whether ecological and economic parameters might serve to predict variation in naturalization and invasion success. Although that work is not begun in the present work, one study demonstrates the importance of climate, propagule pressure, and phylogenetic propinquity in predicting establishment success among alien reptiles and amphibians (Bomford et al., 2005, in press). Examination of a wider array of ecological attributes seems likely to improve predictive success in this regard, which would be useful for screening proposed deliberate introductions for likely invasiveness.

We have seen that islands are more prone to herpetological naturalization than are continents. Although not directly investigated here, it is possible that this pattern reflects the easier invasibility of these relatively depauperate areas.

It is also clear that a wide variety of damaging impacts has resulted from herpetological invasions, even though only a relative handful of naturalized populations has been examined in any ecological or economical detail. It is beyond contention that herpetological invasions can result in tremendous damage to other native fauna, broader ecosystem values, human health, and human economies.

What remains to be determined is how general such impacts are – a question that cannot now be addressed because of the sparse taxonomic sampling of existing impact studies.

Finally, we have seen that effective eradication and control of invasive herpetofauna can be achieved, but only under circumstances that have rarely yet been met. In particular, biological attributes of many reptiles and amphibians have intersected with limited human perception and imagination to virtually ensure failure of most eradication and control operations under present response paradigms. More often response has not even been attempted. Some of the human limitations contributing to this poor record may be overcome with concerted attention, research, and education, and future control operations may meet with improved success. However, the political impetus for such change has largely been lacking so far.

These discoveries have numerous implications for devising proper policy and management responses to herpetological invasions. They also illustrate important research needs.

Implications for Management

What implications do the data presented herein have for design of effective management strategies for alien reptiles and amphibians? And, beyond that, what requirements must be met more generally to respond to this accelerating ecological problem? How can we transcend the current haphazard responses to herpetological incursions and devise an intelligent, coordinated means to significantly reduce this threat?

Perhaps the conclusion of greatest management importance derived from the data presented herein is that prevention of additional herpetofaunal invasions must rely first and foremost on curtailing introductions. This is not only because prevention is the most efficient and (typically) cost-effective means of controlling alien invasions generally (see Chapter 1) but also because eradication and control operations against alien herpetofauna have proven remarkably ineffective to date. Many tens of thousands of additional herpetological introductions are possible (and likely, without change in our habits), and eradication or control will not be a biologically or fiscally viable option for most of them. So averting the problem instead of treating it after the fact will be key. This is not to say that eradication and control operations should be foresworn, but development of effective techniques will require considerable investments in research, and these strategies are unlikely to be widely useful for the foreseeable future. In contrast, pathway-management techniques are either already in hand to some extent or could be developed with less delay and cost. Such techniques include wholesale screening and/or treatment of arriving cargo. Comprehensive prevention programs will necessarily rely largely on the activities of governments because those are the institutions responsible for controlling ingress and egress across political boundaries. However, private programs can also have a role in meeting prevention needs, as discussed later.

In managing pathways for alien herpetofauna, the distinction between intentional and unintentional introductions is of great importance. This is because tactical methods and social requirements will vary for each of those two pathway modes. Hence, it is important to know by which pathways species are most likely to reach a jurisdiction. Most major taxonomic groups of organisms have the majority of their introductions accounted for by only one or a few pathways, typically either accidental or deliberate. For example, marine invertebrates largely travel unintentionally via ballast water or by fouled ship hulls (Fofonoff et al., 2003), and most plants have been moved deliberately for agricultural, silvicultural, or horticultural purposes (Mack, 2003). Birds have largely been moved intentionally via the pet trade and for game hunting, and mammals (except for rats and mice) largely intentionally for game hunting and food or fur use (Kraus, 2003c). In contrast, we have seen that both deliberate and non-deliberate pathways are important in dispersing reptiles and amphibians (Figs. 2.15, 2.36). Given that mixed pattern, it is unsurprising that the taxa moved deliberately are usually different than those moved unintentionally. What this means practically is that preventing further incursions of alien reptiles and amphibians will require a greater diversity of prevention tools than are needed for many other taxa – tools appropriate for both intentional and unintentional pathways. Screening systems to evaluate proposed importations and educational programs to elicit more responsible behavior from the pet-keeping public will be key to effectively reducing deliberate introductions. Improved implementation of inspection programs for high-risk cargo and development of bulk treatment methods for high-risk cargo must underlie any abatement of accidental introductions. And bulk treatment methods are likely to prove useful in stopping a variety of other pests too. Crucial to both will be educational efforts to make clear to the public and government officials why the impacts of alien herpetofauna warrant this attention.

Important too is recognition that pathway importance is not static. Instead, it unambiguously varies taxonomically, temporally, and geographically. What this means is that appropriate intervention tools must be correspondingly flexible. Chronological trends indicate that, overall, pet-trade, cargo, and nursery-trade pathways are increasing in importance; therefore, stemming invasions via these routes will clearly be high-priority goals in many regions for the foreseeable future. But pathway importance also varies geographically, and different countries will need to tailor their prevention activities to reflect the pathways of greatest import to their own jurisdictions. For example, the nursery trade is clearly the single greatest contributor to the movement of alien herpetofauna in the Caribbean and must be addressed if further incursions are to be halted there. That same trade makes a negligible contribution to Europe's influx of alien herpetofauna, which is instead closely tied to the pet trade and the deliberate actions of private herpetoculturists. These fundamental facts of pathway heterogeneity must be understood and incorporated into management planning if meaningful prevention of further herpetological incursions is to be achieved.

What then is logically required to incorporate these basic facts into management programs? At a minimum, one needs detailed risk assessment – assessment

of the major pathways relevant for any particular jurisdiction, and assessment of individual species (or genera) proposed for deliberate introduction. The former would ideally be done at the scale of particular jurisdictions – typically countries, but sometimes island groups or other areas showing regional biotic differentiation – because the geographical analyses used here are too coarse-grained to accurately assess pathway variation within most regions. The United States will be an exception to that rule, however, because the large majority of my data for North America comes from that country. In some cases – such as small countries – there may be insufficient data to generate country-specific risk assessments. In those cases, the regional analyses provided here may be of surrogate use in determining cargo-inspection priorities. That may be appropriate in much of the Caribbean, for example, because the greatest recent risk for many countries in the region has proven to be infested nursery shipments from southern Florida. More usually, though, one would desire country-specific statistics indicating volume of relevant trade items likely to harbor hitch-hiking herpetofauna. Ideally, if one could identify economic statistics that correlate well with transport likelihood for alien herpetofauna, one could use those statistics to set inspection priorities. This is especially likely to hold true for nursery shipments because climatic discrepancy between origin and destination is not likely to be a confounding factor. For other cargo types, information on cargo origin would also factor into risk determinations inasmuch as climatic disparity between origin and destination might obviate successful transport of many species.

Risk assessment for particular species proposed for deliberate introduction (typically as pet animals) may prove difficult to achieve because of the vast diversity of biological idiosyncracies among the total pool of imported/importable herpetofauna. However, as discussed earlier, progress has been made in assessing establishment risk and invasion risk for a diversity of vertebrates, including herpetofauna (Bomford et al., in press), so broad-scale rules are likely to provide some discriminatory assistance. Those findings suggest that great scope remains for developing a usefully predictive screening algorithm, but insufficient attention has been devoted to that effort, so effective screening tools are currently lacking for most jurisdictions.

Preventing introduction cannot, however, be the sole strategy for minimizing future herpetological invasions for the simple reason that no single prevention method is perfect. Although current control technologies for alien herpetofauna are frequently inefficient or poorly developed, in the longer term technological improvements should be achievable, making eradication and control increasingly viable and sensible options for managing some invasive herpetofauna. However, there will remain relevant biological constraints (crypsis, high demographic rates of increase) likely to bar application of these methods to many species. And fiscal constraints on control programs will remain common. Eradication and control operations can logically be done by any form of institution, but government action will often be key because governments are frequently the only entities that can bring a sufficiency of resources to bear on such problems. As well, governments readily provide a logical nexus around which actions of a variety of

interested partners may be coordinated. For these reasons, much of the discussion in this chapter necessarily focuses on governmental management responses and how to improve those. Nonetheless, it should be understood that nothing logically requires that response actions be monopolized by government entities (with the obvious exception of border protection per se), and responsible actions taken by private organizations and individuals can help considerably in reducing alien herpetofaunal invasions.

Critical for future herpetofaunal control operations must be the adoption of a new professional mentality. In particular, pro-active research, comprehensive planning, sufficient funds, and dedicated personnel trained in wildlife control are indispensable – a point repeatedly made in the literature and explicitly adopted in the many successful mammal eradications that have occurred over the past 20+ years (Veitch and Clout, 2002; Nogales et al., 2004; K. Campbell and Donlan, 2005; Howald et al., 2007). The current state of the art with herpetofaunal eradication attempts is far from this standard. Indeed, one is frequently struck by the ad hoc nature of many such eradication operations. This is not a reflection on the personnel engaged in these operations, who are often researchers having little outside support, no tested or refined tools at their disposal, and no wildlife-control experience. These researchers have merely responded out of desperation to try to correct conservation problems facing native animals that have been ignored by responsible agencies. The successful eradication of *Limnodynastes dumerili* from New Zealand (Whitaker and Bejakovich, 2000), *Rana catesbeiana* from Great Britain (Fisher and Garner, 2007), and at least two of three *Xenopus laevis* populations from the United States (Tinsley and McCoid, 1996) may be exceptions to the general pattern of eradication failure in large part because eradication was placed in the hands of conservation-management professionals. Expecting researchers to fix these ecological messes is to rely on the gratis services of people with the wrong sets of skills. To date, resources have rarely been devoted to finding and professionally applying viable eradication or control methods to address herpetofaunal invasions.

Of course, merely developing predictive tools for risk assessment or for control/eradication does not guarantee that they will be vigorously (or even sensibly) implemented by governments or other parties. As an obvious illustration of this, useful predictive tools for screening deliberate plant introductions have been available for over a decade but have been implemented only in Australia and New Zealand (although interest in their application has recently grown in some other jurisdictions, c.f., Gordon et al., 2008). Following the pattern for alien invasions generally, there has been a particular reluctance to act against herpetological incursions on the part of most governments. As noted in the last chapter, some of this derives from disbelief that alien reptiles and amphibians constitute real ecological or economic problems that warrant social response. But this reluctance is more general than just disbelief, sometimes occurring even when the undesirability of the alien species is acknowledged.

This points to the little-discussed management issues of political will and political organization, the presence and structure of which determine the effectiveness of all

invasive-species management efforts, including the successful and failed eradication attempts discussed in Chapter 4. These topics are sufficiently important that they deserve some detailed consideration. Generally speaking, there has been slowly growing appreciation of the ecological and economic seriousness of alien invasions in recent years; however, with few exceptions, governmental engagement with the problem in most jurisdictions has remained of limited scope and effectiveness. The importance of political will and organizational structures in determining a country's invasion fate is perhaps most easily illustrated by contrasting the different approaches taken by two countries possessing the fiscal and intellectual resources required to respond to the challenge competently.

New Zealand has had legislation since 1993 that explicitly places responsibility for preventing and responding to new alien-species invasions in a single governmental authority, the Ministry of Agriculture and Forestry (MAF). Prevention policy in New Zealand includes comprehensive lists of prohibited species and rigorous inspection of arriving cargo and passengers, with inspection priorities based on risk assessment of cargo type and origin. Animals proposed for importation must have an explicit import policy developed by MAF; otherwise, entry is prohibited. Reptiles and amphibians in the pet trade are strictly limited, with most species prohibited from import. When species successfully circumvent preventive detection, new incursions are assessed for hazard and are liable to rapid eradication by MAF. Should eradication fail, control of established pests may then be undertaken by MAF for agricultural pests, by Department of Conservation on their conservation lands (ca. one-third of the country), or by regional councils in accordance with regional pest-management strategies developed with public input. Declaration of a species as a pest often carries the requirement that landowners suppress the species on their lands. Responsibility for preventing alien incursions and eradicating incipient populations is clearly assigned to a single ministry in New Zealand, ultimately making the Minister of Agriculture and Forestry accountable for overall border protection. The only political appointee in this chain of command is the Minister of Agriculture and Forestry, duly elected to Parliament and appointed as a cabinet member by the prime minister. All other relevant officials responsible for biosecurity are permanent professionals of the civil service. Partly as a result of this unified, comprehensive biosecurity system, New Zealand has not had a new species of reptile or amphibian become naturalized since the 1960s.

The United States provides a striking contrast. As mentioned in the last chapter, importation of reptiles and amphibians is virtually unregulated, except that brown treesnakes and three species of African tortoises are prohibited from unlicensed import, which may be allowed for scientific or educational use. Ownership of particular species may also be prohibited by some states. Inspection of arriving cargo is directed toward finding agricultural pests (United States Department of Agriculture, or USDA) or smuggled goods (Customs Department). The United States Fish and Wildlife Service (USFWS) inspects declared shipments of imported animals to verify import declarations are accurate, and it collates importation information to meet CITES requirements. Smuggled animals discovered by Customs are also referred to USFWS for prosecution, largely to enforce CITES requirements.

Hitch-hiking herpetofauna are largely ignored by USDA but may be referred to state agriculture officials should a state have an interest in their interception (this sometimes occurs in Hawaii, for example). With the exception of brown treesnakes, three tortoises, and unlicensed CITES-protected species, no alien herpetofauna are prevented entry to the United States, so prohibition, risk assessment, and cargo inspection for other species liable to be invasive are not required. Further, the Lacey Act, the primary legislative vehicle for prohibiting invasive vertebrates entry into the United States, has been shown to be highly ineffective unless used before a species is ever imported (Fowler et al., 2007). It has, however, more often been used (ineffectively) to ban further import of species already present or established in the country. Should a species naturalize in the United States, control responsibilities are not mandated but might be undertaken by a host of federal, state, or private interests. Primary responsibility for wildlife management lies with states, but many states have no staff herpetologist and no mechanism for addressing invasive reptiles or amphibians. Federal involvement is mandated only if the invader causes a native species to become endangered, but by then the infestation is well advanced and generally irreversible. Some of the applicable agencies may work at cross purposes – for example, states have sometimes promoted the deliberate introduction of species banned by adjacent states. Hence, a state that will ultimately suffer from the range expansion of an introduced reptile or amphibian will have no say in eradication of an infestation arising in another state. Research on alien species, including alien herpetofauna, may of course be undertaken by any interested party. But such research is not an assigned responsibility for any particular government agency and is generally undertaken only in response to a colonization. To the best of my knowledge, no federal agency has accepted responsibility for researching the prevention of reptile or amphibian invasions. The number of different agencies having some hand in invasive-species issues in the United States is approximately 36–40 (National Invasive Species Council, 2005; C. Dionigi, National Invasive Species Council, personal communication, 2007). Instead of having a single federal management authority responsible for preventing alien incursions and responding to those incursions that do occur, the United States defaults instead to a patchwork of dozens of agencies and programs whose jurisdictions may overlap but often fail to connect. Because it is in the nature of bureaucracies to pursue their particular mandates and vigorously defend their jurisdictions, cooperation among this assortment of agencies can be difficult to achieve. Lastly, in the United States, political appointees extend much farther down the executive structure than in New Zealand. Cabinet members (secretaries), deputy secretaries, under secretaries, assistant secretaries, and bureau directors are all political appointees, providing 3–4 layers of political appointees above the permanent civil service. Below this is the senior executive service, whose members serve at the pleasure of the political appointees. This heavy layering of appointees makes decisions based on political interference or accommodation far more likely to occur than in New Zealand, and consistent policy and programmatic development by civil-service professionals is correspondingly constrained and liable to change with changing administrations. These systematic weaknesses have been recognized for some time (Office of Technology Assessment, 1993),

but Congress has responded only by proposing (and occasionally passing) legislation addressing one small facet of the alien invasion crisis at a time. One result of this dystopian approach has been at least 110 naturalizations of reptiles and amphibians in the United States since the 1960s.

This contrast in approaches taken by New Zealand and the United States may be further clarified by considering each country's most successful operations against alien herpetofaunal incursions. As discussed earlier, New Zealand quickly and successfully eradicated an incipient invasion of *Limnodynastes* frogs in 1999, surveying and treating a large area of the Waitakere Ranges within a few weeks (Whitaker and Bejakovich, 2000). The United States has no such success (or even attempt) at rapid eradication of a new herpetofaunal incursion. The United States does, however, have a successful program for containing the highly invasive brown treesnake to Guam (see Chapter 4), thereby protecting other Pacific islands from further invasions by this pest. One measure of this program's success is that brown treesnake sightings in Hawaii declined from eight in the period 1981–1994 (0.57 snakes/year), to one dead animal since the program has been fully functional (0.077 snakes/year). Despite this demonstrable success, the program has existed for its entire 14-year tenure without base funding, that is, it has continued solely on year-to-year funding liable to termination at any time by Congress. But base funding is generally required for the hiring of government employees (as opposed to temporary contractors). Further, no single agency is accountable for the program. As a result, funding flows have been intermittent, especially from the Department of Defense, which is responsible for the majority of departing vehicular traffic on Guam and, correspondingly, poses the largest threat of snake dispersal to other Pacific islands. Hence, even though the brown treesnake prevention program on Guam has been a clear operational success—the only herpetological example that the United States can point to—inadequate administrative design has subjected it to repeated funding crises throughout its history, making it perennially liable to unintended failure.

The administrative contrast between New Zealand and the United States with respect to taking the risk of alien invasions seriously and assigning clear responsibility for responding to them couldn't be more stark. And this is reflected in their recent invasion histories. Some of the difference in naturalization success between the two countries could, of course, be due to the presence in the United States of warmer regions more equable to invasion by alien herpetofauna. But New Zealand does not lack for hospitable habitat, and this certainly does not provide a complete explanation. Instead, the fact that New Zealand has responded to the threat of alien invasions in a coordinated manner largely free of political interference for the past 15 years while the United States has limped along with piecemeal, uncoordinated actions is certainly key to explaining the different on-the-ground results. Particularly important is the fact that New Zealand has largely prohibited trade in pet reptiles and amphibians whereas the United States has no meaningful import restrictions on animals available for private ownership. The importance of this point is confirmed by data from Australia, which has also prohibited private trade in alien herpetofauna and which is unique among the regions surveyed in Chapter 2 in having most

of its alien introductions consisting of internal movement of herpetofauna in cargo (Fig. 2.29). Introductions via the pet trade have been virtually non-existent in Australia. And that country and New Zealand are the least invaded of all Western countries. In contrast, Europe, North America, South America, and Asia all have the majority of their reptile and amphibian introductions occurring via pet-trade releases, and regulation of that pathway is virtually absent in those regions.

The difference in approach and effectiveness between the United States and New Zealand has historical roots. As suggested by Gordon Rodda, the ecological histories of the nations certainly play a role. New Zealanders are very familiar with the heavy toll taken by introduced mammals in their land, and many native species today are famous taxonomic curiosities to be seen only on offshore islands where introduced mammals are lacking. Commitment to invasive-species management is high among both the public and government sectors in New Zealand. Similar histories in Australia and Hawaii have no doubt made each of those jurisdictions similarly sensitive to invasives. In contrast, the iconic stories of wildlife conservation in North America revolve around elimination of bison, passenger pigeons, and a variety of other species at the hand of human gunners. Concern with those losses led to passage of the Lacey Act (primarily protecting native wildlife but subsequently prohibiting some alien animals) and creation of the national wildlife refuge system. Invasive-species issues and reptile and amphibian conservation consequently have had much less historical salience among the American public.

Much of the programmatic ineptness in the United States would appear to be the historical baggage of bureaucratic structures: it would no doubt be politically charged to attempt to reorganize the quagmire of agencies that deal to one extent or another with alien species. This could perhaps reflect a diseconomy of scale, with the United States Government too large and unwieldy to respond to any social problem with dexterity and finesse. If true, greater delegation of prevention and management responsibilities away from the federal government and toward regional and local structures might help improve invasive-species responsiveness in the United States. Similarly ineffective bureaucracies may have hindered responses to invasives in European countries too, which historically have been lax in managing alien reptiles and amphibians. It could be that the political upheaval involved in forming the European Union may now allow scope for devising effective management programs across that region by forcing attention to the issue and setting minimal standards of action. Recent European planning and control activities against alien herpetofauna suggest that such might be the case. Alternatively, the European Union might instead also be approaching a diseconomy of scale as well as expanding its fragmentation of authorities among several hierarchical levels (EU/nations/provinces/municipalities). Hence, it remains too early to be certain whether response effectiveness will be embraced in Europe as it has been in Australia or New Zealand. In any event, ineffective bureaucracies having no clear line of responsibility have certainly served to hinder meaningful management of invasive herpetofauna (and many other species) in a wide variety of countries, including the United States.

A final difference in approach between New Zealand and the United States is that the former explicitly adopts the precautionary principle in devising policies pertaining to alien species. This allows policymakers to opt for excluding a species or eradicating an alien in the absence of scientific certainty of its invasiveness. In contrast, the United States excludes only species known to be pests elsewhere. The precautionary approach assigns burden of proof for safety to the importer, whether the introduction is intentional or a statistically predictable accidental component of legal cargo transport. Under this paradigm, instances of scientific uncertainty are decided in favor of avoiding invasion costs. In contrast, under a reactionary paradigm, burden of proof to demonstrate species risk falls on those social institutions, organizations, or individuals challenging a proposed introduction, and instances of scientific uncertainty are decided in favor of allowing the importation to proceed. Because invasiveness is so difficult to conclusively demonstrate a priori for most species, and impossible for species not previously imported, the reactionary approach defaults to unfettered importation of virtually all biota. With respect to reptiles and amphibians, this problem is particularly acute for the pet-trade pathway. The relentless search for novelty in the exotic pet trade intersects with the reactionary regulatory paradigm to ensure that regulations only prevent the importation of species that were formerly popular as pets and have already become naturalized. This results in a predictably high rate of invasions in countries adopting such a regulatory paradigm. Regulated industries understandably prefer a reactionary approach, as it allows them to externalize the costs of invasive species management. Part of the reason New Zealand and Australia have more successfully responded to the threat of alien invasions is because their governments have recognized these previously externalized costs, attempted to measure them, and responded so as to minimize them.

An additional reason for governmental inaction has been inadequate information. There is often bewilderment among even concerned officials about how to respond to herpetological invasions because control techniques have not previously been reported in the literature or encountered by politicians or agency personnel. And there are few experts that may be consulted for advice on how to respond to such invasions. (As one example, the response to the invasion of South Florida by Burmese pythons relies heavily on expertise from the brown-treesnake program, potentially limiting staff availability for both programs.) In the absence of clearly prescribed solutions, few officials have the clout to devote scarce institutional resources to programs with an uncertain outcome. This leaves inaction as the default (non-) response position. This unhelpful circumstance is potentially amenable to research directed to developing standard control/eradication procedures for reptiles and amphibians, much as has been achieved for rodents in the past three decades.

The point of dwelling at some length on these contrasts in bureaucratic structures and response approaches is that one can identify minimal organizational standards and requirements for effective governmental response to invasive aliens, including invasive herpetofauna. These include combining responsibility for alien prevention and eradication in a single agency with clear accountability and professional

staff protected from political tampering. Further required is explicit adoption of a precautionary approach in responding to alien species. This, in turn, requires an honest economic reckoning of who in society gains from unfettered import and who pays the costs. Finally are needed clear development and explication of effective response options for concerned government officials. Meeting these minimal standards has allowed New Zealand to lead the world in provision of biosecurity protection from invasive aliens, including reptiles and amphibians. Australia also closely approximates these standards. What is certain to fail is having alien-response authorities divided among myriad agencies liable to several layers of political appointees. This structural failing is compounded by adopting a reactionary approach to alien species that requires identification of disastrous invasions elsewhere before adopting piecemeal, limited restrictions against a handful of proven pests, and that is predicated on an economic paradigm that hides the complete costs of importations. That latter approach has kept the United States, European Union countries, and most other countries in the world mired in managerial ineffectiveness. It continues to make them liable to an unending cycle of further invasions.

Of primary importance in stemming further herpetological invasions is stanching the flood of introductions via the pet-trade pathway. The practical result of externalizing trade costs – allowing private interests to accrue wealth through the pet trade while foisting the predictable costs of unhindered importation of cheap animals onto the general public – has been an accelerating rash of herpetological invasions, with southern Florida, Hawaii, and the Ryukyu Islands presenting sorry cautionary tales of dishonest market costing gone awry. In most countries, the pet industry has remained unregulated in any way that would meaningfully reduce its large contribution to herpetological invasions. It should be clear from the evidence presented herein that that situation is untenable and should be rectified. Solutions for this problem can no doubt come in a variety of forms but could include governmental regulation prohibiting species deemed prone to invasiveness, improved public education to increase responsibility among pet owners and pet dealers, and bond requirements for wholesalers and zoos to defray the costs of management resulting from institutional release, neglect, or bankruptcy.

Government regulation of any systematic nature may (but need not) await the design of reliable screening protocols for invasiveness, an approach we have seen prove fruitful with respect to plants, fish, birds, and mammals (see Chapter 1). Despite the potential importance of government regulation in stemming the tide of alien pet releases, one often hears claims that this is a counterproductive approach. This largely stems from the common belief that if import restrictions are imposed on a pet-yearning public it will only drive the trade underground. I believe such a claim to be true. The evidence also suggests it to be irrelevant. Australia, for example, has long banned the import for private ownership of alien herpetofauna. And every herpetologist and herp fancier in the country knows that such species continue to be smuggled into that nation and kept by many private enthusiasts. Yet Australia is also the only major developed country not beset by a rash of alien pet releases. The reason is that by driving the trade underground, Australia has made each smuggled

animal that much more valuable, and careless releases and escapes have been kept remarkably low. In short, via regulation, Australia has managed to impose a sufficiently elevated cost to exotic pet ownership that animals are valued highly enough to largely prevent their release to the wild. As a result, it doesn't matter that prevention of smuggling isn't perfect – it's good enough to ensure that captive herpetofauna largely remain captive. And such a structural adjustment to the pet-value system is all that is needed to effectively protect against an introduction pathway run rampant elsewhere.

Such a result might be achieved alternatively by a quota system that makes abundant, cheap animals unavailable (L.D. Wilson and Porras, 1983). In any event, the point is to impose a cost to pet keeping that removes the incentive for careless release or escape. Enforced maintenance standards for wholesale and retail stock – especially in areas, like Florida, subject to hurricanes – could also prevent some unintentional pet-trade releases. Escape by means of such activities has long plagued Florida in particular but has been a contributing factor in several other jurisdictions as well. Revocation of business licenses for wholesale and retail dealers that release animals or allow them to escape could also be considered. Florida has recently adopted stricter regulations for the keeping of venomous reptiles, a handful of large constrictors, and the Nile monitor, *Varanus niloticus* (Florida Fish and Wildlife Conservation Commission, 2007). These regulations include age, experience, caging, disaster-planning, record-keeping, and escape-notification requirements, as well as the requirement to have each animal permanently identified with a surgically implanted passive integrated transponder. These regulations may go some way toward stemming the release of the more dangerous reptile species held in captivity in Florida, but of course, they are silent on the wider phenomenon of reptile and amphibian release in that state.

Despite any such regulatory efforts that might be made, the importance of the pet trade and aesthetic-release nexus in modern herpetofaunal introductions is so large that, for many countries, government cannot be solely responsible for preventing additional herpetofaunal invasions. The problem is too widespread for such an approach to always be viable, and responsibility for its creation is too diffuse. In particular, it is long past due for industry and private individuals to accept responsibility for preventing the ecological damages caused by pet releases and intentional releases for aesthetic gratification. And improved, focused public awareness of the consequences of pet release will be highly important in meeting this goal. Currently, awareness that pet releases pose an ecological problem (as well as typically being inhumane to the released animals) does not appear widespread among the pet-keeping public. One would hope that it should not be too difficult to develop a new ethos by capitalizing on the love that herpetoculturists feel for reptiles and amphibians. In particular, wider appreciation of the impacts that released pets can have on native herpetofauna, coupled with the fact that released pets often soon die from starvation or exposure, should allow for development of a guilt-free and responsible means of disposing of unwanted or burdensome pets. The pet-keeping publics of few, if any, countries attain that reasonable standard of behavior.

One initiative to elicit greater responsibility among the pet-owning public has recently been taken in the United States. There the pet industry launched in 2005 a focused public-education campaign called Habitattitude™ to prevent release of unwanted pets. Educational activities are largely directed to getting the pet-owning public to avoid impulse buying of pets, to make informed decisions about which pets to choose, and to place unwanted pets in other responsible captive situations in lieu of releasing them to the wild (Reaser and Meyers, 2008). Information on how to meet these goals is provided to prospective buyers in participating pet stores and is available on the web sites of industry advisory councils. This program is one sensible response to the flood of releases due to the pet trade, but it is also young, and it remains to be seen how effective it will prove in decreasing releases to the wild. The tremendous success of the anti-littering campaign in the United States in the late 1960s suggests that a widespread public-education campaign can quickly change human behaviors if that campaign is approached with sufficient vigor. This is exactly what is needed in most developed countries to prevent pet release. The Habitattitude™ campaign remains the only attempt to devise a non-regulatory approach to the pet-trade pathway of which I am aware. It may prove deserving of emulation elsewhere, and similar programs may be relevant to the related problem of religious “mercy” releases of alien herpetofauna in Buddhist countries. In any event, greater responsibility by private citizens is crucial to preventing additional introductions and invasions of alien reptiles and amphibians and will likely need to operate in concert with greater regulatory oversight or adoption of means to increase the economic valuation of pets.

Implications for Research

Innumerable gaps remain in our knowledge of herpetological naturalizations and invasions, the factors that determine their dynamics, the magnitude and frequency of their deleterious impacts, and how they might best be prevented and mitigated. Scientific information on invasive reptiles and amphibians lags far behind that available for better-studied taxa like mammals, plants, and marine invertebrates. Many of these knowledge gaps are of critical management importance – not to mention of intrinsic scientific interest – and I have already indicated how they can sometimes serve to justify management inaction.

Before considering how research might best be focused to address these topics, it is worthwhile to consider for a moment the reasons for this mediocre state of knowledge. In large part, these reasons are historical and lie in the intersection of scientific culture with economic motivation. Invasion biology as a subdiscipline of conservation biology is to a significant extent an applied science. And applied biology has historically been discouraged or disparaged in the academic environment, being assigned a low value because it is often not theoretically challenging and does not expand the conceptual boundaries of fundamental scientific understanding. That perception reflects the value system within academia, and that is fair enough. To put

it bluntly, applied herpetologists don't get tenure. As a consequence, research in applied biology has instead developed when outside economic interests have provided an independent incentive for conducting such research. In large part, the reason why invasive mammals, birds, insects, and plants are much better studied than are invasive reptiles and amphibians is because each of those taxa has imposed major economic costs to agriculture or forestry, and entire research industries have formed around the need to mitigate those costs. No such economic incentive has allowed for the development of a mature field of applied herpetology. (An exception is that a few species have occasionally been farmed or harvested for food or skins, and some energy has gone into investigating best farming practices.) As a consequence, herpetology has remained more strictly esoteric than some other disciplines, and the study of herpetological invasions has necessarily relied on the interest of a sparse pool of ecological researchers. Because academic herpetology has historically foresworn concern with invasive herpetofauna, interested amateurs have by default provided much of the basic observational data in the field. However, these individuals have not been well-positioned to provide rigorous scientific analysis of their observations, so reporting standards and meaningful analysis of patterns and process have largely been lacking, leaving the field with a rather mediocre analytical record.

This situation was long worsened by an attitude among many academic researchers that frequently excused herpetological introductions as inconsequential (e.g., L.D. Wilson and Porras, 1983), justifiable because interesting (e.g., Smith and Kohler, 1978), acceptable once sufficiently ancient (e.g., Böhme, 2000), or worthy of wanton promotion under the guise of research having no focused purpose (e.g., Thurow, 1994, 1997, 1999). One consequence of these *laissez faire* attitudes has been to justify in the minds of many herpetological enthusiasts the acceptability of deliberate introductions (e.g., McKeown, 1996), a practice that continues today. Hence, historical academic attitudes melding scientific disinterest with unconcern for consequences have had wider ramifications, infecting less-fastidious minds with the idea that promoting introductions is acceptable. This combination has abetted the quiet explosion of herpetofaunal naturalizations depicted in Chapter 2.

Those earlier attitudes seem to be shifting. With increased acceptance of conservation biology as a valid academic discipline over the past two decades unconcern among many academic herpetologists toward herpetofaunal invasions has thawed. That perceptual shift has been reinforced by recognition of the ecological harm done by brown treesnakes, cane toads, and bullfrogs. Interest has grown too as the theoretical relevance of species invasions to clarifying ecological processes has become more apparent. We are consequently, I think, poised for major advances in the understanding of herpetological invasions. And, the number of studies directed at naturalized populations of reptiles and amphibians has increased greatly in the past decade or so. But virtually all of these studies have been descriptive, and research focused specifically on hypothesis testing and problem solving has remained sparse. Consequently, it seems fitting to inquire how an increased research interest in herpetological invasions might most profitably be directed so as to achieve significant advances in understanding that are relevant for both science and

management. I find it useful to organize the most relevant research issues along the lines adopted by Rejmánek et al. (2005) for plant invasions. Rejmánek and company asserted that five research questions comprise the core of invasion biology and that these questions need to be answered if we are to progress in understanding and controlling invasions. The questions are:

1. Which taxa invade?
2. How fast?
3. What makes ecosystems invisable?
4. What is the impact?
5. How can we control or eradicate harmful invaders?

Let us address for each what research could most profitably be undertaken in the near term to advance understanding and management of herpetofaunal invasions.

Which Taxa Invade?

As noted earlier, knowledge of which factors lead to establishment or invasion success is virtually undeveloped for alien reptiles and amphibians except for the study by Bomford et al. (2005, in press). But a variety of ecological attributes – especially biotic attributes – remains unexamined. Meshaka (2004) noted that most of Florida's established herpetofauna shared a small suite of attributes linked to early and prolonged breeding, broad diet, and tolerance of human disturbance. More broadly, Rodda and Tyrrell (in press) compared ecological features hypothesized to characterize reptiles and amphibians among the three assemblages of urban, pet-trade, and invasive herpetofauna. They found that features hypothesized to favor invasiveness overlapped considerably with those features thought to favor persistence in urban settings and, to a lesser extent, with those that favor selection for the pet trade. This work presents a useful summary of hypotheses that might explain herpetological invasiveness, but statistical tests demonstrating a preponderance of these attributes among naturalized aliens compared to other herpetofauna remain to be done. Such studies are currently hindered by lack of broad summaries of the required ecological information, as well as by the lack of a reasonable means of ranking herpetological invasiveness. Even though a few herpetofaunal species can clearly be pointed to as demonstrably invasive, and others are just as demonstrably not invasive, development of a reliable metric of herpetological invasiveness has yet to be attempted. Indeed, opinions differ as to whether invasiveness should be defined based on ecological impacts or on magnitude and rapidity of range expansion (e.g., Richardson et al., 2000a; Daehler, 2001), although the two likely have a high degree of overlap. Regardless of what definition might be chosen, we currently lack objective criteria for classifying degree of invasiveness among alien herpetofauna. This clearly imposes an unmet precondition for identifying which species invade. Beyond that remains the large body of work to be undertaken in determining whether herpetological invasiveness can be predicted on the basis of species attributes.

How Fast?

There is virtually no information on how quickly herpetological invasions progress. A few quantitative estimates of range expansion have been provided in the literature (e.g., van Beurden and Grigg, 1980; Eastal, 1988; B.L. Phillips et al., 2007 for *Bufo marinus*; Lobos and Jaksic, 2005; Fouquet and Measey, 2006 for *Xenopus laevis*; Locey and Stone, 2006 for *Hemidactylus turcicus*; Rodda and Savidge, 2007 for *Boiga irregularis*), and one can occasionally find comparative snapshots of invaded range size at different stages of an invasion (e.g., Percsy and Percsy, 2002b for *Rana* spp.). But these are insufficient to make general conclusions about range-expansion rates. It is important to recognize that rate of spread can be due both to the invader's inherent ability to negotiate terrain under its own power as well as to secondary, saltational transport of the species by humans. The latter is likely to be operative in many herpetological invasions, including those involving species having an amenity value. This has been a frequent theme among pet-trade introductions in Florida and Hawaii (e.g., L.D. Wilson and Porras, 1983; Meshaka et al., 2004a), for example, and was a major cause of the rapid spread of *Eleutherodactylus coqui* around Hawaii Island (Kraus and Campbell, 2002). Saltational secondary transport by humans can also be important for accidental hitch-hikers, such as *Anolis sagrei* (T. Campbell, 1996a) and a variety of geckos. Because saltational transport by humans will increase the numbers of populations (and therefore the numbers of spreading nodes) of an alien, it can be a major contributor to rate of spread. And, indeed, species arriving into Florida as cargo stowaways were found to be spreading at a faster rate than those introduced intentionally (Butterfield et al., 1997), which may reflect that these species are preadapted to such saltational dispersal. However, intentional introductions to Florida tend to be more recent than the pool of accidental introductions, so comparisons may well be confounded by time since introduction. In any event, range-expansion rates have rarely been measured for alien herpetofauna, and are not easily measured for some, but there are suggestions that interesting differences in spread rates may correlate to invasion pathway. To what extent range-expansion rates might correlate with impacts remains unresearched.

A related issue of some importance is ascertaining to what extent current perceptions that most alien herpetofauna are benign are due to unrecognized lag phenomena. As noted in Chapter 3, herpetofaunal invasions for which the best evidence of impact has yet been adduced average 62 years old. Some alien populations that were dismissed as harmless two or three decades ago (e.g., *Iguana iguana* in Florida) are now viewed as invasive, and *Eleutherodactylus coqui* appeared to persist largely unnoticed in Hawaii for approximately one decade before exploding out of control over a period of only three years (Kraus and Campbell, 2002). These observations suggest that alien herpetofauna may frequently be subject to long lag periods before population growth becomes sufficiently high that they generate concern among scientists or managers. It remains thoroughly unknown what percentage of alien herpetofauna will exhibit lag phenomena, what the modal time period of these lags might be, and what accounts for them (e.g., human misperception vs. real biological limitations).

What Makes Ecosystems Invasible?

Clearly related to lag phenomena is an understanding of the degree to which alien herpetofauna will remain restricted to urban or other highly modified landscapes or eventually prove capable of invading more-or-less native habitats. Alien herpetofauna in Florida have been argued to be strongly associated with disturbed, primarily urban, areas (L.D. Wilson and Porras, 1983). However, virtually all colonizations in Florida (as in most other locales) originated in urban/suburban areas, so insufficient time may have elapsed to assess to what extent the introduced herpetofauna are capable of colonizing native habitats. This is likely true for most jurisdictions inasmuch as the majority of herpetofaunal invasions are quite recent (Fig. 2.1). More species are now known to be invasive in natural habitats in Florida and elsewhere than when Wilson and Porras wrote, suggesting that we can not expect many urban releases to stay put in the long term. And there are few ecological reasons to expect such a pattern to widely hold, despite the fact that many alien reptiles and amphibians clearly are capable of exploiting disturbed habitats created by humans. If lag phenomena are common among these species, then we should see a large increase in number of natural-area invasions over the coming years. There is currently no compelling treatment of this very basic question.

As noted in Chapter 2, small islands appear to be more readily invasible than larger landmasses. It has also been suggested that the high rate of herpetofaunal invasion of South Florida is partly because that region is ecologically insular, being surrounded on three sides by water and on the fourth by the frost line (e.g., Butterfield et al., 1997). But the reasons why islands and island-like mainland areas might be more amenable to herpetofaunal invasion are not yet known. It has been proposed that Guam was especially vulnerable to the brown treesnake because it has a moderate climate suitable for many foreign species, had high densities of many prey species, lacked competing predators, was sufficiently small as to be quickly overrun, and was distant from any other islands that could have provided refuges or recolonization sources for native wildlife (Fritts and Rodda, 1998; Rodda et al., 1999b). Clearly, such attributes apply to many oceanic islands and may serve to explain why such landmasses would be especially vulnerable to herpetofaunal invasions, but systematic tests of these hypotheses have not been conducted for alien herpetofauna. In short, a host of biotic peculiarities characterize island biotas, and it is not clear which of them (or all in concert) allow for easy establishment or invasibility.

Attempts have not yet been made to determine whether size of naturalized herpetofauna correlates negatively or positively with size of native herpetofauna, although that question has been addressed for some other taxa (e.g., Lonsdale, 1999; Sax, 2002). Nor is it clear to what extent ecosystem invasion by herpetofauna is due to the exploitation of untapped resources vs. superior competition for already utilized resources. The result of these knowledge gaps is that it remains unknown whether or why particular geographic regions or ecosystems might be more liable to invasion than others, although several hypotheses are available for testing (see Chapter 1).

What Is the Impact?

This is one area for which some research progress has been made with alien reptiles and amphibians, as detailed in Chapter 3. Nonetheless, as frequently noted throughout this book, research has been decidedly biased toward a handful of species, and investigation into a taxonomically broader sample of naturalized species would be highly desirable. Although a diversity of impacts is already documented for alien herpetofauna, many categories of impact can point to only one or two exemplars. Partly, this reflects the difficulty of collecting ecological impact data for many of these species. This is especially true for demonstrating predation impacts, which are often extremely time sensitive and difficult to detect or demonstrate once native prey are decimated. Yet, it seems likely that the high densities achieved by many alien reptiles and amphibians will make direct effects on prey species and secondary effects on ecosystems more widespread than currently appreciated. Similarly, investigations into health impacts and economic impacts of invasive herpetofauna have just begun, and additional damages are likely to be identified. In short, despite the fact that research on impacts has grown considerably since the 1980s, studies are not yet sufficiently dense to allow us to assess how frequently naturalized herpetofauna are likely to prove damaging. There is likely to be continued political resistance to responding effectively to herpetological invasions until such a rough estimate can be provided, even though the growing number of herpetological “train wrecks” is garnering some increased political attention. Because waiting for continued train wrecks is a poor management paradigm, better scientific understanding of the likely pool and frequency of impacts attendant upon herpetofaunal invasions is critical for better allocation of management efforts.

Additionally, we need to identify the native ranges of a variety of species widely dispersed by humans. This is critical for clarifying the validity and conservation status of some species, the geographic origins of other species, and the native composition of some insular herpetofaunas (c.f., Chapter 3). Such research has already proven important for conservation purposes in some instances (e.g., Iverson et al., 2001), and further instances await elucidation (c.f., Chapter 3, Appendix B). The considered application of sensitive molecular techniques is likely to be most useful for this purpose, but has rarely been applied to these questions in a comprehensive fashion. Until such research becomes more widely undertaken, many instances of presumptive human introduction (Appendix B) will remain speculative. That these speculations are sometimes in error (e.g., Iverson et al., 2001) and can have practical conservation consequences (e.g., Austin et al., 2003; Palkovacs et al., 2003) highlights the importance of this research need beyond its obvious application to basic evolutionary and biogeographical understanding.

How Can We Control or Eradicate Harmful Invaders?

As I've noted repeatedly, control involves prevention, eradication, and population reduction/control, each operating at a different stage of the invasion process. The first

has different knowledge requirements from the last two. For effective prevention, the pathway analyses begun here need to be extended and refined for particular nations or sub-national jurisdictions (e.g., Galapagos) having quarantine programs. Pathway details that might reasonably be added, but which I have ignored, include type and volume of pet trade, quarantine-agency records, trade-good types and volumes, and major trade partners. These more detailed analyses will improve risk estimates for quarantine purposes within particular jurisdictions. Again, these could be supplemented by any predictive correlations that might be identified between economic variables and pathway importance. A few rough estimates of herpetological traffic within cargo exist for limited places and times (e.g., O'Dwyer et al., 2000; Gill et al., 2001), but focused risk assessment for these taxa seems absent.

Research is also needed to identify interdiction methods that can be applied safely and effectively to treat large volumes of cargo. As one example of what is needed, in response to the coqui invasion in Hawaii and the fact that most of its rapid spread around the state was due to transport in potted plants, State officials modified a hot-water drench system (previously used for cleaning cut-flower exports of insect pests) to remove coqui from infested nursery plants. This method kills a variety of other invasive pests (e.g., slugs, earthworms) as well. Broad adoption of that or a closely related technology could prove useful as a general treatment to transform the nursery trade from an extremely dirty pathway to a much safer one. That method, however, is currently applied in few jurisdictions and only for coqui treatment. Similar treatment methods need to be identified and developed for a variety of other high-risk cargo, including cargo containers and vessels.

It is also important to recognize that the modern phenomenon of alien introductions and invasions is not an ineluctable force of nature. It is a choice made by humans – a choice of what to value and what to discount, a choice of when to act or not to act. As such, biological invasions are in many important ways not primarily biological phenomena at all, but social phenomena. Consequently, social research into the drivers of biological invasions is highly relevant but almost wholly lacking, and even acknowledgement of their importance in the biological literature (which comprises the overwhelming majority of literature) on the topic is virtually absent. Of particular importance would be (1) psychological research into the motivations for and constraints upon responsible pet ownership, genesis of aesthetic appreciation for ecosystems, and the myriad other factors that figure into how humans make valuations regarding promulgation of or defense from alien species; (2) social research into how best to apply incentives for responsible individual behavior toward alien species; (3) political science research into improving responsiveness and successful behavior of institutions charged with responding to this problem; and (4) economic research to identify the costs of alien herpetofaunal invasions and any structural incentives that might improve internalization of these costs. Research on the last-named is just beginning for alien reptiles and amphibians; model legislative tools have been developed for effectively responding to the invasive-species threat more generally (C. Shine et al., 2000), but I know of no work addressing the first two fields.

Of very high management importance is devising effective means of locating and removing alien reptiles and amphibians once introduced. Doubtless a large array of different methods will need to be investigated and developed, in accordance with the wide diversity of lifestyles adopted by the target species themselves. The need for such a diversity of approaches has been made clear in the case of the brown treesnake, for which we earlier saw that trapping, barrier, luring, repellent, toxicant, and toxicant-delivery methods have all proven useful and undergone extensive research. Technique diversity will no doubt expand as additional species become targets of concern. But response to herpetological incursions so far has largely relied on existing methods already used by herpetologists to sample their species, and many control attempts have foundered because of initial lack of reliable and efficient tools. A more concerted effort is needed to test and improve current sampling tools and supplement them with novel ones. The sooner that a wide suite of reliable control tools is available for off-the-shelf application, the fewer instances of failed eradication we will have.

It may be that the notion that we need improved means of exterminating certain reptiles and amphibians will be viewed by many people, including herpetologists, as heretical and repugnant. Vociferous opposition to alien mammal eradications by animal-rights activists is frequent (e.g., Simberloff, 2001; Bertolino and Genovesi, 2003; Howald et al., 2005), but I have occasionally witnessed similar resistance to amphibian eradication and control operations as well. I am by no means certain how widespread such sentiments may be among the herpetological research community, but discomfort with killing our favorite organisms may be one reason why some of the most innovative proposals in herpetological management (toxicants and toxicant-delivery systems for brown treesnakes, genetic sterilization for cane toads) have come from non-herpetologists. Although emotional clouding of judgement is to be expected from a certain portion of the general public, one could hope that the herpetological research community would suspend emotional attachment to their study organisms, recognize that several of these are damaging interlopers, and accept that its skills and knowledge are valuable for remedying that ecological hazard. At the very least, one could hope that professional herpetologists would at least abstain from censure or uninformed dismissal of such activities, as has sometimes occurred (e.g., Holden, 2003).

Important too will be further research on the demographic parameters of invasive herpetofauna. Such research, in addition to its intrinsic scientific interest, has the potential to identify stages in a species' life cycle at which it may be especially susceptible to control. Govindarajulu et al. (2005) provide an excellent illustration of how such research may be of practical application.

On a broader note, I suggest that professional herpetologists bear another responsibility that has heretofore been ignored. As I've mentioned before, much literature on invasive herpetofauna is less informative than it could be. Information of broad scientific utility is absent from many (most?) reports. All new reports of introductions or naturalizations should at least address the questions of when the introduction occurred, how many separate introductions were involved, what the relevant pathways were, what personal motives inspired the introduction (if any can

be identified), and what the current status of the population appears to be. In those rare instances when origin or numbers of individual animals involved in the introduction are known, those data should be included as well. For summaries covering numerous escaped or released aliens, specifying the times of their discoveries should be required instead of just giving a broad date range. Of course, not all of these data will be available for all introductions, and publication should not be prohibited in those instances – the last thing we need is another reason to reject applied papers. But reporting standards and use of terminology have been remarkably varied throughout the literature surveyed for this study, and attempts to show that each of these scientifically relevant details were at least considered (if not all liable to resolution) would work considerably to improve the quality of information available to researchers in assessing future trends. A perusal of the database and bibliography will make clear the degree to which *Herpetological Review* has filled the niche in reporting new alien reptile and amphibian populations. *Applied Herpetology* also has a new section devoted to the topic. Adoption of these minimal standards by those journals would set a precedent that could go some considerable way toward improving reporting standards throughout the field.

As I have said above, interest in herpetological introductions and invasions has grown among both researchers and managers in recent years, but this interest has not yet gelled into focused hypothesis testing, problem solving, or effective management. A largely new generation of herpetologists is investigating a greater range of questions and invasive taxa than was the case a mere few years ago. And there is an increasing number of managers and policy makers who wish to address herpetological invasions but have been hindered by lack of reliable information and methodologies. But, with only one or two exceptions (notably, the United States' brown treesnake program and, perhaps, Australia's cane toad program), the research and management communities have not greatly intersected or interacted, so fruitful programs of adaptive management and applied invasive herpetology have not yet matured. I have tried to show how available information is sufficient to justify a greater degree of policy attention to these ecological interlopers than has historically been tendered, and to show as well some of the structural requirements for effective policies and programs to be developed and implemented. I have also pointed toward research areas that are in greatest need of attention from a practical, conservation point of view. Most of these questions also have their own intrinsic scientific interest, which will be obvious enough to scientists, given their training. But I have sought to show how such research might best fit into a practical conservation paradigm and, thereby, have joint impact in both fields. Management uninformed by scientific knowledge will likely prove misguided or counterproductive; research uninformed by management needs will likely remain arcane or sterile. If the conservation impact of herpetological invasions is to be decreased, these two communities need to address singly their respective structural, programmatic, and research gaps and need to work together to better focus their energies on adaptive problem solving. Otherwise, it is difficult to see what will prevent the exponential increase of herpetofaunal naturalizations from thoroughly transforming the communities and ecosystems that we jointly cherish.

Appendix A: Database of Introductions

Database Structure and Content

The database currently includes 2,142 records for 676 taxa. All these records consist of species except for 67 instances that were originally identified only to genus or family. In all cases, a single record consists of an introduction of a particular species to a particular location. Data collected, as available, include (1) species, (2) locality to which introduced, (3) success of the introduction, (4) dates of introductions (including dates for multiple introductions, when known), (5) reason(s) for introduction, (6) minimum number of independent introductions of the same species to the same locality, (7) literature supporting the data in these prior cells, (8) literature providing additional data on the ecology or evolution of the species in the recipient jurisdiction, and (9) taxonomic synonyms. Not all these data are available for all species, but some are available for most. Each field requires some explanation.

1. **Species.** Effort has largely been made to render the species names consistent with the latest accepted taxonomic usage. However, herpetological nomenclature has been in a period of considerable flux in the past decade and I have not incorporated all proposed recent changes. One such exception is that I have not adopted the generic name changes proposed for *Bufo*, *Eleutherodactylus*, and *Rana* by Frost et al. (2006). This is partly because the proposed taxonomic changes haven't stabilized, but also because the changes would make the database presentation totally dissonant with the primary literature for a variety of important introduced amphibian species, making it harder for non-systematists to gain access thereto. Since most users of this database will be non-systematists, I give them priority of consideration. Nonetheless, interested researchers should be aware of these proposed nomenclatural changes and may adopt them for future work, as interested. Changing nomenclature and mistaken identifications sometimes result in conflict between the current name and that used in some of the earlier cited literature. To make it easier for researchers to access that literature, each entry includes under the heading "syn:" synonyms or mistaken names under which the species has been referred in the literature for that jurisdiction, if different from current usage. I cannot guarantee I've identified every alternate

name for every entry, but all relevant alternates should be identified within the pool of locality records for each species. This should facilitate recognition of the older literature passages that differ from current nomenclature.

2. **Locality.** Locality of introduction is typically a defined political jurisdiction, usually a country, but for the United States and Canada I subdivided jurisdiction by state or province. As well, because political jurisdictions are arbitrary, I also tracked data separately for biologically important islands or island groups that are parts of larger, distinct countries. Importance, in this case, was determined by the biogeographical significance of the island or island group irrespective of its current political affiliation. So, for example, records for the Galapagos are treated separately than those for the remainder of Ecuador, those for the Ryukyus separately than for the remainder of Japan, Sardinia and Sicily separate from Italy, etc. Doing this allows for better assessment of the degree to which introductions to islands are more successful than those to continental areas.

I excluded the following from the database: (1) conservation re-introductions to a species' native range; (2) releases of animals from one part of their native range to another, unless a distinctly different genetic lineage (operationally, typically involving a different subspecies) or source population was unambiguously involved; and (3) experimental introductions to tiny unoccupied islands in the midst of a species' native range. The first is irrelevant to assessing the degree to which reptile and amphibian introductions serve as a conservation threat, as opposed to a remedy. The second is usually unknowable and rarely reported in the literature (see Eckstein and Meinig, 1989; Münch, 1992 for exceptions). The third is likely a reflection of colonization or extinction stochasticity, is biogeographically meaningless, and adds nothing to my analyses. So, for example, I do not include in the database experimental introductions of *Anolis sagrei* to several uninhabited islets in the midst of its native range in the Bahamas (Schoener and Spiller, 1996, 1999; Losos and Spiller, 1999, 2005), *Podarcis pityusensis* to Dau Gran in the Balearic Islands (Böhme and Eisentraut, 1981), or *Podarcis sicula* to coastal islands in Croatia (Radovanović, 1959, 1965; Nevo et al., 1972). In each case, the species in question is native to the immediately adjacent mainland or surrounding islands and biogeographic patterns remain unobscured. I do include all other introductions to islands, even if near a species' native range, because the introduction is potentially of some biogeographical significance. For example, I include the introductions of *Podarcis sicula* to the Aeolian Islands of southern Italy and *Sauromalus* species in the Sea of Cortez because in each case biogeographic patterns are potentially obscured by the introduction and/or endemic congeners are potentially affected by the introductions.

These distinctions can admittedly be somewhat arbitrary, and two problematic issues remain, although relatively few taxa are involved. First, I do include in the table introductions of species to areas outside of their historic ranges even if those areas were inhabited prehistorically but modern presence in the area is compellingly ascribed to human introduction. The primary example of this is *Emys orbicularis*, which inhabited virtually all of Europe during xerothermic eras but has been absent

from most of central Europe during historic times. Also, it has recently been proposed that *Rana lessonae* had at least one native historic population in Great Britain (Gleed-Owen, 2000; Beebee et al., 2005; Snell et al., 2005; but see Langton and Burton, 2006, for a contrary opinion) even though current populations derive from introductions. Normally, such an instance would be excluded from Table A.1; however, the introduction is so well-known and documented (and the involved lineages are genetically distinct) that I have elected to include it in the table for the sake of completeness. Second, there is a number of species of questionable introduction status in certain areas, as discussed in Chapter 3. For example, it is widely assumed that most of the geckos and skinks to be found in the eastern reaches of the Pacific (and parts of the Indian Ocean) were introduced by humans (e.g., Beckon, 1992; Moritz et al., 1993; Austin, 1999). Similar claims are made for populations of *Iguana iguana* and *Geochelone carbonaria* in the Caribbean (e.g., Censky, 1988; Corke, 1992) and are becoming rather commonplace for a variety of species on Mediterranean islands (e.g., Böhme and Wiedl, 1994; Corti et al., 1999). As discussed earlier, many of these claims are reasonable on biogeographic, morphological, or genetic grounds but are problematic because direct evidence in support of these claims hasn't been provided in most instances and details delineating native from introduced ranges are lacking for all examples. I am happy to assume that many of these hypotheses will eventually be demonstrated to be correct; nonetheless, I have largely left such instances out of this database for two reasons: (1) the quality of evidence in support of such claims is generally not yet very advanced, and it becomes difficult to justify inclusion of these claims with the same level of confidence that characterizes the other entries in this database, which are based on discovering species unobserved during older surveys, or known with certainty to be foreign, or whose introduction has been directly admitted/observed; and (2) deleting claims of prehistoric introductions, even if they later prove true, has no practical effect on the analytical goals of assessing the modern phenomenon of herpetological homogenization. Exclusion of these relatively few examples is not intended as a curt dismissal of the truth of these claims so much as a desire to await clearer evidence before including them. For some island groups, where evidence of recent introduction is clearer and explicitly presented, I have included these species as introductions even though they may not be listed as such for nearby areas for which compelling arguments have not yet been made.

- 3. Success.** This cell records whether or not the introduction was reported to be established at the time of the most recent literature citation for the population in question. Categories are “yes” if established, “no” if not established, or “?” if the status of the introduction could not clearly be inferred from the literature. Populations that were successfully established for years but later became extinct (e.g., *Podarcis sicula* in Pennsylvania) are included in the database as failures. Including data for both established and unsuccessful introductions was done to assess relative success of introduction pathways and to better assess pathway importance.

4. **Number.** The minimum number of independent introductions of a species to a jurisdiction is given, when known or able to be estimated from the literature. By “independent” I mean separate colonizations from outside the locality in question, including division of a single lot of animals for release into separate areas at the same time. This is meant to exclude the phenomenon of spread of the alien species once successfully established in the new region (whether done by “natural” dispersal of the species or by further saltational movement of animals by humans), although it is possible that I have inadvertently counted as independent introductions a few instances of what are, in reality, translocations of existing stock. It is sometimes difficult to distinguish between the two from the literature available.

Instead of explicitly providing numbers of separate introductions, authors frequently summarize observations of alien herpetofauna verbally as “commonly”, “frequently”, or “occasionally” seen, for example. I have operationally rendered “some”, “occasional”, and “a few” as a minimum of “2”; “several” as “3”, and “many”, “numerous”, “frequent”, or “common” as “4” in the following table. The value in this column frequently defaults to “1” because most authors don’t specify, even in this approximating verbal fashion, the number of introductions they are discussing, especially when considering incidences of escaped or released pets. Sometimes I have been able to estimate a minimum number of introductions by counting numbers of independent introduction locations on maps provided in original articles. In such instances, each location counted as only a single introduction, even though many more may have occurred at some localities. This option could be used, for example, in obtaining numbers of *Trachemys scripta* introductions to some European countries because of active herpetological atlas projects in that region. Again, note that I have adopted a conservative stance in estimating numbers of introductions, so the number given in this column is a bare minimum estimate of introduction intensity based on literature information. It is not intended to be, nor can it be interpreted as, a precise measure of number of introductions because those are impossible to know in most instances. For example, it is impossible to know the real number of times a species such as *Trachemys scripta* has been released (no doubt in the tens or hundreds of thousands) because not all releases are known or reported in the literature. Nonetheless, including a minimum estimate of number of independent introductions does provide some measure of relative propagule pressure across taxa and pathways.

5. **Pathway.** The reason for introduction is included in the database only if explicitly mentioned in one or more of the supporting literature citations or if it could be reasonably inferred from data presented or something said in those citations. For all other instances, even if the general pathway of introduction for a species is well-known, that information cell was left blank. For example, *Ramphotyphlops braminus* has been introduced around the world in nursery materials, and many authors have pointed to this introduction pathway – and to no other – in explaining its recent arrival to their particular geographic area.

But claims for introduction pathway were not explicitly made by some authors for several areas in the introduced range of this species; thus, I did not ascribe a pathway for those areas. Occasionally, species have been repeatedly introduced to a particular jurisdiction for multiple reasons, and in these instances each documented or claimed reason is provided, as well as the minimum number of times that pathway was utilized, if known or liable to estimation. If a single introduction was done for multiple reasons, both are listed within braces. In those few instances in which introduction pathway is uncertain but is narrowed down to a couple options, both options are listed within brackets. Parenthetical numbers following a pathway designation indicate the minimum number of introductions that are claimed or implied for that pathway. If no number is provided, the pathway was either generally mentioned in reference to some introduction but not clearly associated with any particular introduction event (if multiple events occurred), or is unambiguously assigned when only a single introduction occurred. Pathway designations should be self-explanatory with one exception. As explained in Chapter 2, I have used the pathway designation “intentional” to denote those introductions known to have been deliberately made by individuals but without fitting into one of the other deliberate categories of introduction (e.g., for biocontrol or food use). These “intentional” introductions have often been noted or implied as being done out of personal aesthetic interest, but frequently motives are unspecified although likely to derive from some form of aesthetic satisfaction.

6. **Date.** Date of introduction is provided when known or liable to close estimation, whether done explicitly by an original author or done by me based on data an author provided. Dates of single specimens of obvious pet animals that never formed established populations were typically approximated as the date of discovery or the previous year, based on the assumption that most such animals do not survive for extended periods in most jurisdictions. Multiple dates for multiple introductions are recorded when known. Only introductions from outside the boundaries of the jurisdiction in question are included; dates of subsequent dispersal of animals to new localities within the jurisdiction are not tracked. Approximate date of entry into a jurisdiction by normal dispersal of animals from a naturalized population in an adjacent jurisdiction are shown in brackets; those dates were excluded from the pathway analyses.

In the pathway analyses of Chapter 2, dates were grouped by decade, beginning from 1850, so analytic methods are robust to some imprecision in date estimation. In many cases, dates of introduction cannot be estimated or are insufficiently precise to be unambiguously assigned to decade. Such records were excluded from calculations of pathway development through time. I made exceptions for two studies (Kraus and Cravalho, 2001; Eterovic and Duarte, 2002) that each presented many introduction records for a date range that spanned several years of the 1990s but only the first few months of 2000. In those two cases, I counted all introductions as falling into the 1990s so as to increase the data available for analyses. Although this is not exactly correct (one might expect 5 of 76 introductions in São Paulo

and 1 of 18 in Hawaii to be mis-assigned to decade on the basis of chance), the resulting error is too small to compromise the overall patterns shown, but the gain in evidence is large. Introductions prior to 1850 were clustered together as “< 1850” and used to set the Y-intercept for the timeline graphs illustrated in Chapter 2.

7. **Supporting Literature.** Included here are references documenting all preceding data cells for the introduction record as well as references providing information on continued range expansion within the invaded jurisdiction. For many introductions there is some degree of redundancy among these included citations as more recent references repeat the claims of those preceding them. I have deliberately retained this redundancy because it will help ensure that interested researchers can locate at least some of the relevant literature pertaining to any particular introduction of interest. This is important because the primary literature for a large number of introductions resides in a wide array of obscure, frequently regional journals that may be difficult for many interested researchers to obtain. Despite this favorable bias toward some amount of redundancy, I did not strive for an absolutely complete coverage of all possible herpetological books that might mention a particular introduction because I reckon any sensible person will think of these sources without my assistance and because it is becoming impossible to keep up with the flood of regional herp books swamping the market, especially from a bibliographically starved location such as I inhabit. Typically, when I have cited books in the database it is because they provide some amount of novel information for the relevant introduction.
8. **Additional Literature.** Included here are references that were not relevant to populating the main cells of the database but which provide information on ecological attributes, interactions, or impacts, as well as genetics or evolution of the introduced populations. Many of these citations involve brief and fairly uninformative notes that, nonetheless, could be construed as providing a modicum of relevant habitat or behavioral information. A few references are for laboratory behavioral studies that are nonetheless directly relevant to understanding the ecology of the alien populations from which the investigated animals were taken. Citations in this column were included to assist the interested researcher in entering the relevant literature. They also serve to highlight the paucity of studies on these relevant biological topics for the large majority of alien herpetofauna. Perhaps drawing attention to these lacunae may stimulate interest in their diminishment.

I made every effort to have the citations in columns (7) and (8) as complete as possible through 2006. I have also included whatever citations from 2007 that I have incidentally encountered, although I have made no attempt to comprehensively sample the literature after 2006. Excluded from both columns of the literature cited are theses and dissertations. This is because such sources are frequently difficult to obtain but primarily because I figure if the authors can't be bothered to publish their findings I can't be bothered to cite them. Also excluded are articles in newspapers because it would be impossible to capture that information on a global scale. Nevertheless, interested researchers might bear in mind that such sources

could provide additional information that might be relevant to assessing introduction rates and pathways at a local level. For the same reason, I have not included personal communication of unpublished introduction or naturalization events – they simply cannot be captured comprehensively at a global scale. Finally, I have made no sustained attempt to capture the gray literature of government reports. The relatively few exceptions I've made to this rule are for studies that have been repeatedly cited in the literature, are not too difficult to obtain, and provide information not available in the published literature. I believe most of these exceptions are of reports coming from Australia or the United States. Again, interested researchers are likely to find it productive to pursue such reports at their local level.

A note on bibliographic completeness: this published bibliography includes >4,000 literature citations and a brief perusal of the journal titles will indicate the wide range of sources involved. Every effort was made to make this bibliography as complete as possible, given the constraint that I actually see the article (or have a translation provided by a native speaker) myself. This criterion has required me to exclude ca. 70 additional references that I have been unable to find in any library in the United States, Australia, or at the British Museum (Natural History), or to obtain directly from the printer overseas. Most of these unavailable citations derive from the European or Japanese literature (some of these are cited in Lever, 2003) and to note that they are in obscure, difficult-to-obtain regional journals would be an understatement. The important point is that the interested researcher may not find every relevant citation for an introduction included in this bibliography, but they should be able to use the citations so provided to trace back and find the additional missing citations on their own, should they so desire.

Despite my best efforts to avoid them, I have every confidence that some errors and inconsistencies will remain in this database. I hope they will be sufficiently rare that the overall usefulness of the final product is not thereby compromised. I can only apologize for these in advance and note that I welcome learning of mistakes or overlooked literature that I can use to update or correct the database.

Table A.1 Database of introduction records

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
FROGS							
<i>Acris crepitans</i>	US: Colorado	N	1		1957	Livo et al., 1998	
<i>Alytes obstetricans</i>	Great Britain	Y	4	Nursery trade (1), intentional (2)	1903, 1933, 1954	R.H.R. Taylor, 1948, 1963; M. P. Benson, 1980, 1981; P. Smith, 1949, 1950, 1951a; Fitter, 1959; J.F.D. Frazer, 1964; C. Lever, 1977, 1980; M.J.A. Thompson, 1979; Blackwell, 1985; Ely, 1985; Whitlock, 1997; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002	Johnson, 1990
	Italy	?	2	Intentional (1)	1880s (1)	Bruno, 1978	
	Netherlands	Y	5			Grossenbacher, 1997; Krefler, 2001	
	Poland	N	1			Boulenger, 1897	
<i>Aparasphenodon brunoi</i>	Great Britain	N	1	Cargo stowaway	1960s	Yalden, 1965	
<i>Ateolopus zeteki</i>	US: Florida	N	1	Pet trade		W. King & Krakauer, 1966	
<i>Bombina bombina</i>	Austria	Y	1			Sochurek, 1978; Cabela & Tiedemann, 1985	
	Germany	?	1	Pet trade	Late 1980s	Eckstein & Meinig, 1989	
	Great Britain	N	3	Intentional (3)	1890s	Fitter, 1959; J.F.D. Frazer, 1964; C. Lever, 1977, 1980	
(<i>syn. Bombinator igneus</i>)	Malta	N	1	Intentional	1910s	Despott, 1913	
	US: New Jersey	N	1	Intentional	~1964	Rothman, 1965	
<i>Bombina orientalis</i>	Germany	?	3	Pet trade (3)	1985, 1980s (2)	Eckstein & Meinig, 1989; Münch, 1992	
	Netherlands	N	1		1989	Gubbels, 1992	
	Spain	N	1	Pet trade		J. Rivera & Arribas, 1993	
<i>Bombina variegata</i>	Germany	Y	1	Intentional	1978–1982	Tolke, 1996; Szymura, 1998	
	Great Britain	N	2	Intentional (2)	1954, 1964	J.F.D. Frazer, 1964; Coleridge, 1974; C. Lever, 1977, 1980; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002	

<i>Bufo americanus</i>	Italy: Sicily Canada: Newfoundland	Y Y	1 5	Biocontrol (5)	1960, 1963, 1964, 1965, 1966	Bruno, 1978 Buckle, 1971; Maunder, 1983, 1997; F.R. Cook, 1984; C.E. Campbell et al., 2004 Lazell, 1976; Cardoza et al., 1993 G.S. Myers, 1945; Riemer, 1959 W. King & Krakauer, 1966 E.H. Bryan, 1932; Tinker, 1938; Oliver & Shaw, 1953 Pleguezuelos, 2004 Fitter, 1959 Fitter, 1959 Bruno, 1970; Corti et al., 1997
<i>Bufo arenarum</i>	US: Massachusetts	Y	1	Intentional	1945	
<i>Bufo blombergi</i>	US: Florida	N	1	Biocontrol	1960s	
<i>Bufo boreas</i>	US: Hawaii	N	1	Biocontrol	1892	
<i>Bufo bufo</i>	Canary Islands	N	1		1960	
(syn: <i>Bufo vulgaris</i>)	Great Britain	N	5	Intentional (5)	1930s	
	Ireland	N	1	Intentional	Mid-1800s	
	Italy (offshore islands)	N	3		Late 1960s (3)	
(syn: <i>Bufo vulgaris</i>)	Malta	N	1	Intentional	1910s	
(syn: <i>Bufo vulgaris</i>)	New Zealand	N	2	Intentional (2)	1867, 1893	
	Spain	Y	1			Despott, 1913 Thomson, 1922; Archey, 1935; West, 1979; Robb, 1986; B.D. Bell, 1982a, b Fernández de la Cigofía, 1991; Pleguezuelos, 2004
<i>Bufo calamita</i>	Malta	N	1	Intentional	1910s	Despott, 1913
<i>Bufo dhufarensis</i>	Saudi Arabia	Y	1			Balletto et al., 1985; Ramadan & Al Jobair, 1986 Leviton, et al., 1992

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Bufo gargarizans</i> (syn: <i>Bufo bufo miyakonis</i>)	Japan; Ryukyu Islands	Y	4	Biocontrol (3), intentional (1)	1930s, 1975	Matsui, 1975; Toyama, 1984a; Toyama & Ota, 1991; Otani, 1993; Ota, 1995, 1999, 2000; Goris & Maeda, 2004; Ota et al., 2004a; Toda & Yoshida, 2005	H. Hasegawa, 1984, 1989
(syn: <i>Bufo asiaticus</i> , <i>Bufo bufo</i>)	US: Hawaii	N	1	Biocontrol	1895	Svihla, 1936; Tinker, 1938; Oliver & Shaw, 1953	
<i>Bufo gutturalis</i> (syn: <i>Bufo regularis</i>)	Mauritius	Y	1	Biocontrol	<1870	Bour & Moutou, 1982; Cheke, 1987; Tonge, 1990	Starmühlner, 1976, 1979
(syn: <i>Bufo regularis</i>)	Réunion	Y	1	Biocontrol	1927	Bour & Moutou, 1982; Cheke, 1987	Starmühlner, 1979
<i>Bufo japonicus</i>	South Africa	Y	1			de Villiers, 2006a	
	Japan: Izu Islands	Y	1			M. Hasegawa, 1999; Toda & Yoshida, 2005	
<i>Bufo marinus</i> (syn: <i>Bufo agua</i>)	Japan: mainland	Y	4			Goris & Maeda, 2004; Toda & Yoshida, 2005	
	American Samoa	Y	1	Biocontrol	1953	American Samoa, Office of the Governor, 1953; Simmonds, 1957; Eastel et al., 1981a; Amerson et al., 1982; Eldredge, 2000; G.S. Grant, 2002	Goldberg & Burse, 1992; G.S. Grant, 1995, 1996
	Anguilla	N	1			Hodge et al., 2003	

Antigua	Y	I	Biocontrol	<1916	Clark, 1916; Lynn, 1957; Eastal, 1981; Eastal et al., 1981b	van Buurt, 2006
Aruba	Y	I	Intentional	Early 1960s	van Buurt, 2005	Froggatt, 1935; Mungomery, 1936b; Goodacre, 1947; Ormsby, 1955; Hewitt, 1956; Wilhoff, 1960; Breeden, 1963; Pockley, 1965; Warburg, 1965; Yuen, 1965; Inglis, 1968; Fellows, 1969; C.R. Johnson, 1972; Mawson, 1972; Lyon, 1973; van Tets & Vestjens, 1973; Waterhouse, 1974; Covacevich & Archer, 1975; L.J. Bennett, 1978; Hutchings, 1979; van Beurden, 1980, 1981; Sabath, 1981; Stammmer, 1981; Floyd, 1983, 1984; R. Harding & Catterall, 1983; Shine & Covacevich, 1983; Floyd & Benbow, 1984; Freeland, 1984, 1985, 1986b, 1987, 1994; Bekker, 1985; Eastal, 1985a, b, 1986, 1989; Hamley & Georges, 1985; Liggins & Grigg, 1985; Delvinquier, 1986;
Australia	Y	14	Biocontrol (14)	1935-1937 (14)	Anonymous, 1935; Mungomery, 1935a, 1936a, 1937; A.F. Bell, 1936, 1939; Kinghorn, 1938; Straughan, 1966; Rayward, 1974; Boughton & Sabath, 1980; Tyler, 1980; van Beurden & Grigg, 1980; Eastal, 1981, 1988; Floyd et al., 1981; Sabath et al., 1981; Hughes, 1982; Eastal et al., 1985; Freeland & Martin, 1985; Eastal & Floyd, 1986a; Freeland, 1986a; S. Lewis, 1989; Ingram & Longmore, 1991; Seabrook, 1991; Limpus et al., 1999; Gillespie & Clemann, 2000	van Buurt, 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
						Freeland & Kerin, 1988;	
						Edmonds, 1989; Fitzgerald, 1990; Ingram & Covacevich, 1990; O'Shea et al., 1990; Speare, 1990; Zahari et al., 1990; Cribb & Barton, 1991; M.K. Jones, 1991; Shine, 1991; Clerke & Williamson, 1992; Covacevich & Couper, 1992; Barton, 1993, 1994, 1997, 1998; Cohen & Alford, 1993, 1996; Seabrook, 1993; Werren & Trenergy, 1993; Alford, 1994; Angus, 1994; Durette-Desset et al., 1994; Speare et al., 1994, 1997; Alford et al., 1995, 2006; D. Mitchell et al., 1995; Duignan, 1996; Guinand & Easteal, 1996; Seabrook & Dettmann, 1996; Schwarzkopf & Alford, 1996, 2002, 2007; Sutherst et al., 1996;	
						Burnett, 1997; Lawler & Hero, 1997; Crossland, 1998a, b, c, 2000, 2001; Crossland & Alford, 1998; Lampo & De Leo, 1998; Slade & Moritz, 1998; Sue & Platt, 1998; Zupanic et al., 1998;	

Crossland & Azevedo-Ramos, 1999; Catling et al., 1999; Seebacher & Alford, 1999, 2002; Williamson, 1999; Caudell et al., 2000; Komak & Crossland, 2000; Leblois et al., 2000; Tikel et al., 2000; Berger et al., 2001; Estoup et al., 2001, 2004; A.D. Thomas et al., 2001; Lampo, 2002; van Dam et al., 2002; Altman et al., 2003; Fearn, 2003; B.L. Phillips et al., 2003, 2004, 2006, 2007; Boland, 2004a, b; Donato & Potts, 2004; B. Phillips & Fitzgerald, 2004; B.L. Phillips & Shine, 2004, 2005, 2006a, b, c; Letnic & Ward, 2005; McRae et al., 2005; C. Miller, 2005; Murray & Hose, 2005; R. Taylor & Edwards, 2005; J.K. Webb et al., 2005; G.P. Brown et al., 2006; Doody et al., 2006a, b; Greenlees et al., 2006; Grigg et al., 2006; Hagman & Shine, 2006, 2007; Molloy & Henderson, 2006; Shine et al., 2006; J.C. Smith & Phillips, 2006; Woinarski et al., 2006; Semeniuk et al., 2007; Urban et al., 2007

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Australia: Norfolk Island	?	1		1999	Covacevich et al., 2001	
	Barbados	Y	1	Biocontrol	~1833	Schomburgk, 1848; Gosse, 1851; Waite, 1901; Clark, 1916; Bayley, 1950; C. Grant, 1959; Easteal, 1981; Easteal et al., 1981b	Tucker, 1940; Everard et al., 1988
(syn: <i>Byffo agua</i>)	Bermuda	Y	1	Biocontrol	1885	F.C. Waite, 1901; Verrill, 1902; Barbour, 1914; Pope, 1917; Dunn and Conant, 1937; Wingate, 1965; Easteal et al., 1981b	Metcalf, 1923; R.W. Williams, 1959, 1960; Goldberg et al., 1995a; Linzey et al., 1998a, c, 2003; Bacon et al., 2006a, b; Fort et al., 2006a, b
	British Virgin Islands	Y	1			Easteal et al., 1981b; MacLean, 1982	
	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	
	Canouan	Y	1			Daudin & de Silva, 2007	
	Carriacou	Y	1	Cargo stowaway	1998	C. Lever, 2001, 2003; Daudin & de Silva, 2007	
	Cayman Islands	Y	1		~1994	Burton & Echternacht, 2003	
	Chagos Archipelago	Y	1		1978–1979	Barnett & Emms, 1997; C. Lever, 2001, 2003	

CNMI	Y	3	Biocontrol (3)	1939-1941 (2), 1944	<p>Loveridge, 1945; Stohler & Wiles & Guerrero, 1996 Cooling, 1945; Townes, 1946; Downs, 1948; V.M. Tanner, 1948; Gressitt, 1954; R.P. Owen, 1974; Eastéal, 1981; Eastéal et al., 1981a; Eldredge, 1988; Wiles et al., 1989; Rodda et al., 1991; McCoid, 1999</p>
Cook Islands	N	1		1986	Eldredge, 2000
Cuba	N	2	Biocontrol (2)	1935, 1946	<p>Bruner, 1935; Jaume, 1966; Burde, 1967; Eastéal, 1981; Eastéal et al., 1981b; Garrido & Jaume, 1984; Estrada & Ruibal, 1999</p>
Dominica	N	1			<p>Eastéal, 1981; Eastéal et al., 1981b; C. Lever, 2001;</p>
Dominican Republic	Y	1		<1937	<p>Mertens, 1938; Cochran, 1941; Eastéal, 1981; Eastéal et al., 1981b; Powell et al., 1999</p>
Egypt	N	1		1937	Eastéal, 1981
Fiji	Y	1	Biocontrol	1936	<p>Jack, 1936; Simmonds, 1937; R.J.A.W. Lever, 1937, 1942; Pernetta & Wating, 1979; Eastéal, 1981; Eastéal et al., 1981a; C. Morrison, 2003</p>
					<p>R.J.A.W. Lever, 1937, 1938a, b, c, 1939; Simmonds, 1937, 1957; Turbet, 1938; Hineckley, 1963; Fischthal & Kuntz, 1967; Gorham, 1968; Delvinguier & Freeland, 1988a</p>

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
FSM		Y	2	Biocontrol (2)	1939–1940, 1946	Townes, 1946; Fisher, 1948; Gressitt, 1954; Jackson, 1962; Eastal, 1981; Eastal et al., 1981a; Ashby, 1983; Eldredge, 1988, 1994; Crombie & Pregill, 1999	
Grenada		Y	1		1870s	Barbour, 1914; Eastal, 1981; Eastal et al., 1981b	Everard et al., 1980, 1983; J.M. Germano et al., 2003
Guadeloupe		Y	1			Schwartz & Thomas, 1975; Eastal, 1981; Eastal et al., 1981b; Breuil, 2002	Jourdane & Theron, 1975; Nassi & Dupouy, 1988
Guam		Y	2	Biocontrol (2)	1937 (2)	Anonymous, 1937a, b, d, e, 1938; Loveridge, 1945; Townes, 1946; A.G. Smith, 1949; Gressitt, 1954; Eastal, 1981; Eastal et al., 1981a; Eldredge, 1988, 1994, 2000; Rodda et al., 1991; McCoid, 1993a, 1999; Perry et al., 1998b	Anonymous, 1937c, 1940; Swezey, 1941; Nafus & Schreiner, 1989; Haddock et al., 1990; Haddock & Nocon, 1993; McCoid, 1994; Goldberg et al., 1999
Haiti		Y	1		1932	E.E. Williams et al., 1963; Eastal, 1981; Eastal et al., 1981b; Powell et al., 1999	

(syn: *Bufo agui*)

Jamaica	Y	1	Biocontrol	1844	Gosse, 1851; Waite, 1901; Barbour, 1914, 1937; Dunn, 1926; Lynn & Grant, 1940; Lynn & Dent, 1943; Goin & Cooper, 1950; Eastéal, 1981; Eastéal et al., 1981b; Crombie et al., 1984	Metcalf, 1914, 1923; G.B. Thompson, 1950; Metrick & Dunkley, 1968; Wong & Bundy, 1985
Japan: Ogasawara Islands	Y	1	Biocontrol	1949	Matsumoto et al., 1984; Ota, 2000; Goris & Maeda, 2004; Nakajima et al., 2005; Toda & Yoshida, 2005	Matsumoto et al., 1980; Kusano et al., 1991; Kanube, 2004a, b, 2006
Japan: Ryukyu Islands	Y	1	Biocontrol	<1940	Matsui, 1975; Eastéal, 1981; Eastéal et al., 1981a; Matsumoto et al., 1984; Toyama, 1984a; Maeda & Matsui, 1989; Toyama & Ota, 1991; Ota, 1995, 1999, 2000; Uchiyama et al., 2002; Goris & Maeda, 2004; Ota et al., 2004a; Masunaga et al., 2005; Nakajima et al., 2005; Toda & Yoshida, 2005	
Kiribati	?	1			Lever, 2001	
Line Islands	?	1			Lever, 2001	
Marshall Islands	N	1			Lever, 2001	
Martinique	Y	1		<1844	Gosse, 1851; Waite, 1901; Barbour, 1937; Eastéal, 1981; Eastéal et al., 1981b	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Montserrat	Y	1		<1879	Barbour, 1914, 1937; Eastal, 1981; Eastal et al., 1981b	
	Mustique	Y	1	Cargo stowaway	2003	Paice, 2005; Daudin & de Silva, 2007	
	Nevis	Y	1		<1914	Barbour, 1914, 1937; Eastal, 1981; Eastal et al., 1981b; Lever, 2001	
	New Zealand	N	4	Cargo stowaway (4)		Gill et al., 2001; Anonymous, 2005	
	Palau	Y	1	Biocontrol	Late 1940s	Gressitt, 1952, 1954; Savage, 1960; Eastal, 1981; Eastal et al., 1981a; Crombie & Pregill, 1999	
	Papua New Guinea	Y	2	Biocontrol (2)	1937 (2)	Anonymous, 1939; R.J.A.W. Lever, 1942; W.C. Brown, 1952; Menzies, 1975, 1996; Pippet, 1975; Zug et al., 1975; Eastal, 1981; Eastal et al., 1981a; Eldredge, 1999	Anonymous, 1968; Zug et al., 1975; Bailey, 1976; Menzies & Tapilatu, 2000
	Philippines	Y	1	Biocontrol	1934	R.J.A.W. Lever, 1938a; Rabor, 1952; Eastal, 1981; Eastal et al., 1981a; C. Lever, 2003	Rabor, 1955; Alcalá, 1957; Babudieri et al., 1973

(syn: <i>Bufo agui</i>)									Dexter, 1932; Leonard, 1933; Seán, 1937; Wolcott, 1934a, b, 1937, 1948, 1950a, b; Hoffman & Janer, 1941; Cofresi-Sala & Rodríguez de Vega, 1963; Heatwole et al., 1968; Carpenter & Gillingham, 1984, 1987; Burrowes et al., 2004; Vargas-Salinas, 2005, 2007
Puerto Rico	Y	3	Biocontrol (3)	1920, 1924, 1926	1920, 1924, 1926	Wolcott, 1924, 1935; Danforth, 1925; May, 1926, 1927, 1930; C. Grant, 1931; Leonard, 1933; Tucker & Wolcott, 1935; Van Volkenberg, 1935; Perez, 1951; Rivero, 1978; Easteal, 1981; Easteal et al., 1981b; R. Thomas & Joglar, 1996			
Puerto Rico: Culebra	Y	1		1970s		Rivero & Joglar, 1979			
Solomon Islands	Y	1	Biocontrol	1940		R.J.A.W. Lever, 1942; Loveridge, 1945; V.M. Tanner, 1948, 1951; W.C. Brown, 1952; Easteal, 1981; Easteal et al., 1981a			R.J.A.W. Lever, 1945; Cain & Galbraith, 1957; Fischthal & Kuntz, 1967; Hines, 2000
St. Kitts	Y	1		<1904		Barbour, 1914, 1937; Easteal, 1981; Easteal et al., 1981b			
St. Lucia	Y	1		<1879		Barbour, 1914, 1937; Easteal, 1981; Easteal et al., 1981b			
St. Vincent	Y	1		<1916		Clark, 1916; Easteal, 1981; Easteal et al., 1981b; Censky & Kaiser, 1999; Lever, 2001			
Taiwan	N	1		1935		R.J.A.W. Lever, 1938a; Kaburaki, 1939; Easteal, 1981; Easteal et al., 1981a; C. Lever, 2003			Takano & Iijima, 1937a, b, 1939

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Thailand	N	1	Zoo trade	1975	Tyler, 1975; Easteal, 1981; C. Lever, 2003	
	Tuvalu	Y	1		1939	R.J.A.W. Lever, 1942; Easteal, 1981; Easteal et al., 1981a	
	U.S. Virgin Islands	Y	2	Biocontrol (2)	<1883, 1934	C. Grant, 1937; Philibosian & Yntema, 1976; Easteal, 1981; Easteal et al., 1981b; MacLean, 1982; Platenberg & Boulton, 2006	McManus & Nellis, 1975
	US: Arizona	?	1		1970s	Howland, 1996	
	US: California	N	1		1936 (2)	Jemmings, 1987a, 2004	
	US: Florida	Y	7	Biocontrol (4), pet trade (3)	1936 (2), early 1940s, early 1950s (2), 1963, 1964	Lobdell, 1936, 1937; Neill, 1957; Allen & Neill, 1958; Duellman & Schwartz, 1958; Riemer, 1959; W. King & Krakauer, 1966; Krakauer, 1968, 1970a; S. Austin, 1975; Layne et al., 1977; Easteal, 1981; Easteal et al., 1981b; L.D. Wilson & Porras, 1983; D. Stevenson & Crowe, 1992a; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2004a; Hero & Stoneham, 2005; Krysko et al., 2005; Himes, 2007	T.R. Alexander, 1965; Krakauer, 1968, 1970b; Rossi, 1983; Okafor et al., 1984; J.C. Lee, 1986, 2001; Meshaka, 1993, 1994c; Oliver et al., 1993; B.K. Roberts et al., 2000; Punzo & Lindstrom, 2001; J.C. Lee & Corrales, 2002; K.G. Smith, 2005a, b; Meshaka et al., 2006a

US: Hawaii	Y	1	Biocontrol	1932	Anonymous, 1932; Leonard, Pemberton & Williams, 1933; Pemberton, 1933, 1934; Mungomery, 1935b; Tinker, 1938; Fisher, 1948; Oliver & Shaw, 1953; Hunsaker & Brese, 1967; Eastaek, 1981; Eastaek et al., 1981a; McKeown, 1996	Anonymous, 1932; Leonard, Pemberton & Williams, 1938; Anonymous, 1941; Illingworth, 1941; Arnold, 1944; Fullaway & Krauss, 1945; Brock, 1948; La Rivers, 1948; Pemberton, 1949; Baldwin et al., 1952; Tanada & Beardsley, 1958; Yuen, 1965; Hinton & Dunn, 1967; Eastaek, 1985a; R.W. Slade & Moritz, 1998; Barton & Pichelin, 1999; Estoup et al., 2001; Barton & Riley, 2004
					van Volkenberg, 1935	
US: Louisiana	N	1			Cardoza et al., 1993	
US: Massachusetts	N	1		1991	Astudillo & Arano, 1995; Mateo, 1997a;	
Spain	Y	1		~1900	Barbadillo et al., 1999; Pleguezuelos, 2004	
					Tyler, 1975; AQIS, 2002	
<i>Bufo melanostictus</i>	N	2	Cargo stowaway (2)	1974, 2002		
Australia	N	2		<1991	Malkmus, 1993, 2000;	
Indonesia: Sulawesi	Y	2		1980-1999	Iskandar & Tjan, 1996	
Indonesia: West Papua	Y	1			Menzies & Tapilatu, 2000	
Maldiv Islands	Y	1			Gardiner, 2006; Moutou, 1985	
Mauritius	N	1		1837	Laidlaw, 1903; Mertens, 1934; Cheke, 1987	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	New Zealand	N	2	Cargo stowaway (2)		Gill et al., 2001	
<i>Bufo regularis</i>	Egypt	Y	1	Cargo stowaway	1990s	Ibrahim, 2001b; Baha el Din, 2006	
<i>Bufo schneideri</i> (syn: <i>Bufo paracnemis</i>)	US: Florida	N	1	Biocontrol	1945	G.S. Myers, 1945; Riener, 1959	
<i>Bufo stomaticus</i>	Sri Lanka	N	1	Cargo stowaway	1932	Kirtisinghe, 1957; Dutta & Manamendra-Arachchi, 1996; C. Bambaradeniya, 5/2/01, personal communication	
<i>Bufo viridis</i>	Balearic Islands	Y	1	Cargo stowaway	<1000BC	Alcover & Mayol, 1981; Hemmer et al., 1981; Salvador & Pérez Mellado, 1984; Tonge, 1986; J. Rivera & Arribas, 1993; Esteban et al., 1994; Mateo, 1997a; Mayol & Román, 1997; Palerm, 1997; Barbadillo et al., 1999; Mayol, 2003; Pleguezuelos, 2004	Balcells, 1955a; Vidal, 1965, 1966; Hemmer & Kadel, 1981; Muntaner, 1999
	Great Britain	N	1	Intentional	1958	R.H.R. Taylor, 1963; J.F.D. Frazer, 1964	
	Italy (offshore islands)	Y	7			Bruno, 1970; Lanza, 1973; Corti et al., 1997; Lillo, 2006	
	Malta	N	1	Intentional	1910s	Despott, 1913	

	Russia	Y	1				Zolotareenko, 1985; Kuzmin, 1994
	Spain	Y	1				Rodríguez-Aguilera & Goncé, 1986; López-Higuera et al., 1989; Hernández Gil et al., 1993
<i>Bufo woodhousei</i>	US: Florida	N	1				Netting & Goin, 1945
<i>Bufo</i> sp.	Great Britain	N	1				Yalden, 1965
bufonid sp.	New Zealand	N	1				Gill et al., 2001
<i>Cophixalus ornatus</i>	Australia	N	1				Czechura, 1995; Low, 2003
<i>Crinia signifera</i>	Australia	N	1				O'Dwyer et al., 2000
<i>Dendrobates auratus</i>	US: Hawaii	Y	1				Ullman, 1967; Daly et al., 1992; B.K. Chan et al., 2007
							Hunsaker & Breese, 1967; McMorris, 1970; McKeown, 1996; Kraus & Duvall, 2004
<i>Discoglossus pictus</i>	France	Y	3				Boulenger, 1897; Wintrebert, 1908; Fretey, 1975; Krünyjens et al., 1979; Lanza et al., 1986; Geniez & Cheylan, 1987; Martens & Veith, 1987a; Lanza, 1989; Hafner, 1997; Veith & Martens, 1997; Arnold & Ovenden, 2002; Duguet & Melki, 2003; Fradet & Geniez, 2004; Pascal et al., 2006
							Martens & Veith, 1987b; Veith & Martens, 1987, 1992; Glaw & Vences, 1991; Zangari et al., 2006
							Boulenger, 1897; Wintrebert, 1908; Fretey, 1975; Krünyjens et al., 1979; Lanza et al., 1986; Geniez & Cheylan, 1987; Martens & Veith, 1987a; Lanza, 1989; Hafner, 1997; Veith & Martens, 1997; Arnold & Ovenden, 2002; Duguet & Melki, 2003; Fradet & Geniez, 2004; Pascal et al., 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Great Britain	N	2	Intentional (2)	1930s, early 1960s	Lantz, 1947; J.F.D. Frazer, 1964; C. Lever, 1977, 1980	
	Spain	Y	1	Spread from adjacent introduction	[Late 1800s]	Martínez Rica, 1983; Lanza et al., 1986; Martens & Veith, 1987a; Llorente et al., 1995, 1997a, 2004; Mateo, 1997a; Barbadillo et al., 1999; Pleguezuelos, 2004; Franch et al., 2007	Montori & Fèlix, 1989; García-París & Jockusch, 1999; García-París et al., 2004
<i>Discoglossus sardus</i>	France	N	1	Research	1955	Haffner, 1997; Pascal et al., 2006	
<i>Dyscophus guineti</i>	Spain	N	1	Pet trade	2001	Pleguezuelos, 2004	
<i>Eleutherodactylus antillensis</i>	Panama	Y	1	Intentional	1969	De Sousa et al., 1989	
(syn: <i>Eleutherodactylus portoricensis</i>)	U.S. Virgin Islands	Y	1	Intentional	1930s	C. Grant, 1937; Grant & Beatty, 1944; R. Thomas, 1966	
<i>Eleutherodactylus cochranæ</i>	Puerto Rico: Isla Palominos	N	1	Research	1965	Levins & Heatwole, 1973	
<i>Eleutherodactylus coqui</i>	Dominican Republic	Y	2	Intentional, nursery trade		Joglar & Rios-López, 1998	
	Guam	N	2	Nursery trade	2003, 2004	Beard & Pitt, 2005; Christy et al., 2007a, b	
	Puerto Rico: Culebra	Y	1		1970s	Rivero & Joglar, 1979; Joglar, 1998	

(syn: <i>Eleutherodactylus portoricensis</i>)	Puerto Rico: Vieques	Y	1		Joglar, 1998
	U.S. Virgin Islands	Y	5	Nursery trade (5)	1960s, 1970s
					R. Thomas, 1966; Philibosian & Yntema, 1976, 1977; MacLean, 1982; Platenberg & Boulon, 2006; Waddle et al., 2006
(syn: <i>Eleutherodactylus martinicensis</i>)	US: California	Y	1		Beard & Pitt, 2005
	US: Connecticut	N	1		Beard & Pitt, 2005
	US: Florida	Y	1	1972	D.F. Austin & Schwartz, 1975; L.D. Wilson & Porras, 1983; Loftus & Herndon, 1984; Dalrymple, 1994; Bartlett & Bartlett, 1999; Meshaka et al., 2004a
	US: Hawaii	Y	1	Nursery trade	~1987
					McKeown, 1998; Kraus et al., 1999; Loope et al., 2001; Kraus and Campbell, 2002
					E.W. Campbell & Kraus, 2002; Beard & O'Neill, 2005; Beard & Pitt, 2005, 2006; B.A. Kaiser & Burnett, 2006; Woolbright et al., 2006; Goldberg et al., 2007; Vélo-Antón et al., 2007; Sin et al., 2008
	US: Louisiana	N	1		Conant & Collins, 1991; Dundee, 1991; Schwartz & Henderson, 1988, 1991

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Eleutherodactylus gosseii</i> (syn: <i>Eleutherodactylus luteolus</i>)	Bermuda	N	1		1890s	Pope, 1917; Dunn & Conant, 1937; Wingate, 1965, 1969; H. Kaiser, 1997; Bacon et al., 2006b; Fort et al., 2006b	R.W. Williams, 1959
<i>Eleutherodactylus johnstonei</i>	Anguilla	Y	1	Nursery trade	Mid-1980s	Censky, 1989; H. Kaiser & Hardy, 1994; Hodge et al., 2003	
	Aruba	Y	1	Nursery trade	Early 1990s	van Buurt, 2005, 2006	
(syn: <i>Eleutherodactylus martinicensis</i>)	Barbados	Y	1		1879	Fielden, 1889, 1903; Bayley, 1950; C. Grant, 1959; Schwartz, 1967; Marsh, 1983; H. Kaiser & Hardy, 1994; H. Kaiser, 1997	Lemon, 1971; Everard et al., 1990; Ovaska, 1991a, b, 1992; Ovaska & Humte, 1992
	Barbuda	Y	1			H. Kaiser, 1997	
	Bequia	Y	1	Intentional	1969	Lazell & Sinclair, 1990; H. Kaiser & Hardy, 1994; Lazell, 1994; Daudin & de Silva, 2007	
(syn: <i>Eleutherodactylus martinicensis</i>)	Bermuda	Y	2	Nursery trade	<1880	Pope, 1917; Dunn & Conant, 1937; Wingate, 1965, 1969; H. Kaiser & Hardy, 1994; H. Kaiser, 1997; Bacon et al., 2006b	R.W. Williams, 1959; Watkins et al., 1970; Goldberg et al., 1995b; Linzey et al., 1998b, c, 2003
	Bonaire	Y	1	Nursery trade	1996	van Buurt, 2005, 2006	
	Canouan	Y	1		Early 2000s	Daudin & de Silva, 2007	

Carriacou	Y	1		Early 2000s	Daudin & de Silva, 2007
Colombia	Y	2	Intentional, nursery trade	Late 1980s	Ruiz-Carranza et al., 1996; Ortega et al., 2005a, b Rueda-Almonacid, 1999; Acosta-Galvis, 2000; Ortega et al., 2001; H. Kaiser et al., 2002
Costa Rica	?	1			Savage, 2002
Curaçao	Y	1	Nursery trade	1970s	Hardy & Harris, 1979; H. Kaiser & Hardy, 1994; van Buurt, 2005, 2006
Dominica	Y	1	Cargo stowaway	1979	Bullock & Evans, 1990; H. Kaiser, 1992, 1997; H. Kaiser & Hardy, 1994; Corke, 1992; H. Kaiser & Wagenseil, 1995
French Guiana	Y	1	Nursery trade	>1970	Lescure & Marty, 1996
Great Britain	N	1	Nursery trade	1885	A. Günther, 1895; Hardy & Harris, 1979; H. Kaiser & Hardy, 1994
Grenada	Y	1		~1885	Barbour, 1914; Schwartz, 1967; H. Kaiser & Hardy, 1994; H. Kaiser, 1997; Williamson et al., 2002
Guadeloupe	Y	1		1960s	Schwartz et al., 1978; Hardy & Harris, 1979; Hardy, 1985; Henderson et al., 1992; H. Kaiser & Hardy, 1994; H. Kaiser, 1997; Breuil, 2002

(syn: *Hylodes martinicensis*)

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Guadeloupe: Marie-Galante	Y	1		1899	Henderson et al., 1992; H. Kaiser & Hardy, 1994; Breuil, 2002	H. Kaiser & Henderson, 1995
	Guyana	Y	1		<1919	Hardy & Harris, 1979; Lescure, 1983; H. Kaiser & Hardy, 1994	G.R. Bourne, 1997, 1998
(syn: <i>Elutherodactylus martinicensis</i>)	Jamaica	Y	4	Biocontrol (4)	1890 (2), 1894 (2)	Barbour, 1910a; Dunn, 1926; Lynn & Grant, 1940; Perkins, 1942; Lynn & Dent, 1943; Jeffrey-Smith, 1946; Schwartz & Fowler, 1973; Schwartz & Henderson, 1991; H. Kaiser & Hardy, 1994; H. Kaiser, 1997	Goin & Cooper, 1950; Pough et al., 1977; Stewart, 1977; Stewart & Martin, 1980; H. Kaiser & Henderson, 1994
	Martinique	Y	1		1960s	Lescure, 1966; Lescure & Marty, 1996; H. Kaiser, 1997	H. Kaiser & Henderson, 1994
	Mustique	Y	1		1990	Henderson et al., 1992; H. Kaiser & Hardy, 1994; Daudin & de Silva, 2007	
	Panama	Y	1	Nursery trade	Mid-1980s	Ibáñez & Rand, 1990; H. Kaiser & Hardy, 1994; H. Kaiser, 1997	
	Petit St. Vincent	Y	1			Daudin & de Silva, 2007	

St. Barts	Y	1	Nursery trade	1995	Breuil, 2002; Lorvelec et al., 2007
St. Lucia	Y	1			Lescure & Marty, 1996; Lescure, 2000
St. Vincent Trinidad	Y Y	1 3	Cargo stowaway (2), research	1970s, 1979, 1990	Lescure, 2000 Hardy & Harris, 1979; Kenny, 1980; H. Kaiser & Hardy, 1994; H. Kaiser, 1997
Union Island	Y	1		1990	Henderson et al., 1992; H. Kaiser & Hardy, 1994; H. Kaiser, 1997; Daudin & de Silva, 2007
US: Michigan	N	1			Zippel et al., 2005
Venezuela	Y	1	Nursery trade	1958	Hardy & Harris, 1979; Rada de Martínez, 1982; Gorzula, 1989; La Marca, 1992; H. Kaiser & Hardy, 1994; Manzanilla Puppo et al., 1995; H. Kaiser, 1997; Barrio Amorós, 1998, 2001; Gorzula & Señaris, 1998; H. Kaiser & Grismer, 2001; H. Kaiser et al., 2002; Rojas-Runjaic et al., 2007
<i>Eleutherodactylus mar- tinicensis</i>	Y	1	Nursery trade	>1970	H. Kaiser, 1992

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Eleutherodactylus planirostris</i>	St. Martin	?	1	Nursery trade	1980s	Breuil, 2002	
	Grenada	Y	1			H. Kaiser, 1992; Kraus et al., 1999	
(syn: <i>Euthyas planirostris</i>)	Guadeloupe	N	1	Nursery trade	1997	Breuil, 2002	
	Guam	Y	1	Nursery trade	2003	Christy et al., 2007a, b	
	Jamaica	Y	2	Cargo stowaway		Lynn, 1937; Lynn & Grant, 1940; Lynn & Dent, 1943; Goin, 1947; Schwartz & Fowler, 1973; Schwartz, 1974; Stewart, 1977; Pough et al., 1977	C.B. Lewis, 1943; Goin & Cooper, 1950; Pough et al., 1977; Stewart & Martin, 1980
	Mexico: Veracruz	Y	1			Schwartz, 1974; Flores-Villela, 1993	
	Turks & Caicos Islands	Y	1			Schwartz & Henderson, 1991	
	US: Alabama	Y	1			S.D. Carey, 1982	
(syn: <i>Eleutherodactylus ricordii</i> , <i>Lithodytes ricordii</i>)	US: Florida	Y	1	Cargo stowaway	1863	Cope, 1863, 1875, 1889; Barbour, 1910b, 1937; Stejneger & Barbour, 1917, 1933; Van Hynning, 1933; Harper, 1935; Carr, 1940; Goin, 1944, 1947; Duellman & Schwartz, 1958; Reichard & Stevenson, 1964;	Deckert, 1921; Skermer, 1939; Neill, 1951a, b; D.S. Lee, 1969; H.W. Campbell & Christman, 1982; Muthinsky, 1985; Dalrymple, 1988; Lips, 1991; Dodd, 1992; Meshaka, 1993, 2001; Engé & Wood, 2000; Meshaka & Layne, 2002, 2005

W. King & Krakauer, 1966; Schwartz, 1974; Layne et al., 1977; L.D. Wilson & Porras, 1983; Lazell, 1989a; Franz, 1995; J.B. Jensen & Palis, 1995; Butterfield et al., 1997; Enge, 1998; Bartlett & Bartlett, 1999; Irwin, 1999; Krysko & Reppas, 1999; Wray & Owen, 1999; Christman et al., 2000; Krysko & King, 2000a; Meshaka et al., 2000, 2004a; Irwin & Irwin, 2001; Irwin et al., 2001; S.A. Johnson et al., 2003a; Lillywhite & Sheehy, 2004

US: Georgia
 US: Hawaii

US: Louisiana

Y
 Y
 Y

1
 1
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Nursery trade
 Nursery trade

1998
 1992
 1975

Winn et al., 1999
 Kraus et al., 1999; Kraus and Campbell, 2002
 Plotkin & Atkinson, 1979; Dundee & Rossman, 1989; Dundee 1994; Platt & Fontenot, 1995, A.A. Williams & Wýgoda, 1997; Boudny, 1998, 2004; Elbers, 2007; Liner, 2007

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Eleutherodactylus unis-trigatus</i>	US: Mississippi Ecuador: Galapagos Islands	Y ?	2 1	Nursery trade	2003 2000	Dinsmore, 2004 H.L. Snell, 2000	
<i>Eleutherodactylus</i> sp. (syn: <i>Eleutherodactylus portoricensis</i>)	Great Britain US: Florida	N N	1 1	Cargo stowaway Intentional	1960s 1960s	Yalden, 1965 W. King & Krakauer, 1966	
<i>Euphlyctis ehrenbergii</i>	Saudi Arabia	Y	1	Lab release		Balletto et al., 1985; Leviton, et al., 1992	
<i>Fejervarya cancrivora</i>	Guam	?	1	Aquaculture con-taminant	2003	Christy et al., 2007a, b	
<i>Fejervarya cancrivora</i> (syn: <i>Limnonectes cancrivora</i>)	Indonesia: West Papua	Y	2			Menzies, 1996	
<i>Fejervarya limnocharis</i>	Guam	?	1	Aquaculture con-taminant	2003	Christy et al., 2007a, b	
	Japan: mainland	Y	3			Uchiyama et al., 2002; Toda & Yoshida, 2005	
<i>Fejervarya</i> sp. (syn: <i>Rana limnocharis</i>)	Japan: Ryukyu Islands	Y	4	{Biocontrol + research (1)}, pet trade (2)	Early 1920s (2), 1930s, 1952	Ota, 1983, 1995, 1999, 2000; Chigira, 1988; Toyama & Ota, 1991; Toyama, 1998; Nakata, 2001; Ota et al., 2004a; Toda & Yoshida, 2005	
<i>Gastrophryne carolinensis</i>	Bahamas	Y	1	Nursery trade	1972	Jacobs, 1973a; Crother, 1985; D.S. Lee, 2004, 2005	

<i>Hoplobatrachus chinensis</i> (syn: <i>Hoplobatrachus rugulosus</i> , <i>Rana rugulosa</i>)	Cayman Islands	Y	1	Nursery trade	1986	Schwartz & Henderson, 1991; Seidel & Franz, 1994
<i>Hoplobatrachus tigrinus</i> (syn: <i>Rana tigrina</i>)	Malaysia: Sabah	Y	1	Food	1960s	Matsui, 1979; Inger & Lian, 1996; Inger & Stuebing, 1997
	Philippines	Y	1		1990s	Alcala & Brown, 1998
	Laccadive Islands	Y	1			Gardiner, 1906
	Madagascar	Y	1			Guibé, 1953; Andreone et al., 2003; Raselimanana & Vences, 2003; Vences et al., 2003a
<i>Hyla arborea</i>	Great Britain	N	14	Intentional (9), pet trade (2)	1840s, 1906 (2), 1933, 1937, 1952 (2), 1954, 1955	R.H.R. Taylor, 1948, 1963; C.A. Snell, 1984, 1985, 1990 M. Smith, 1951a; Fitter, 1959; J.F.D. Frazer, 1964; Yalden, 1965; C. Lever, 1977, 1980; C.A. Snell, 1991; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002
	Malta	N	1	Intentional	1910s	Despott, 1913
	Russia	N	1			Kuzmin et al., 1996
<i>Hyla cinerea</i>	Germany	?	3	Pet trade (3)	1980s (3)	Münch, 1992

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Puerto Rico	Y	1	[Cargo stowaway, pet trade]	1963	Philibosian & Yntema, 1977; Rivero, 1978; Meshaka, 1996a; R. Thomas & Jøglar, 1996	
	US: Kansas	N	1	Aquaculture contaminant	1974	Collins, 1993	
	US: Massachusetts	N	1	Nursery trade	1991	Cardoza et al., 1993	
	US: Missouri	Y	1			T.R. Johnson, 1987	
	US: Texas	Y	2	Cargo stowaway, pet trade	<1930, 2006	A.H. Wright & Wright, 1949; Conant, 1977; Leavitt et al., 2007	
<i>Hyla intermedia</i>	Switzerland	Y	1			Dubey et al., 2006	
<i>Hyla japonica</i>	Japan: Izu Islands	Y	1			M. Hasegawa, 1999	
	Russia	N	1		Early 1970s	Kuzmin et al., 1996	
<i>Hyla meridionalis</i>	Balearic Islands	Y	1			Alcover & Mayol, 1981; J. Rivera & Arribas, 1993; Esteban et al., 1994; Barbadillo et al., 1999; Pleguezuelos, 2004	Galeano et al., 1990
	Belgium	N	1	Intentional		Percy & Percy, 2002a	

(syn: <i>Hyla arborea</i>)	Canary Islands	Y	1	<1890s	Steindachner, 1891; Bertin, 1946; Bischoff, 1985; López-Jurado, 1991; Mateo, 1997a; Barbadillo et al., 1999; Pleguezuelos, 2004	Cott, 1934; H. Schneider, 1978, 1981, 1982, 1985; Gerhardt & Schneider, 1980; M.R. Baker, 1981; Mobbs, 1981; Voggenreiter, 1985; Carrera-Moro et al., 1987a, b; Luis & Báez, 1987, 1988, 1990; Rogner & Voigt, 1987; Galeano et al., 1990; Rogner, 1992; Trujillo & Barone, 1995; Evenhuis, 2006
	France	Y	1	1930s	Knoepfler, 1961, 1973; Fretey, 1975; Cheylan, 1983; Hafner, 1997; Duguet & Melki, 2003	
	Germany	N	1	1980s	Bammerlin & Bitz, 1996	
	Great Britain	N	2	Intentional (2)	J.F.D. Frazer, 1964; C. Lever, 1977	
(syn: <i>Hyla arborea</i>)	Madeira	Y	1	Mid-1800s	Sarmiento, 1948; Báez, 1993; Malkmus, 1995; Arnold & Ovenden, 2002	
	Spain	Y	3	Boat (2), intentional (1)	1976 (1), 1990s (1)	García-París & Martín Albadalejo, 1987; García-París et al., 1989; J. Rivera & Arribas, 1993; Pleguezuelos, 2004
<i>Hyla squirella</i>	Bahamas	Y	1		Crombie, 1972; D.G. Campbell, 1978; D.S. Lee, 2004, 2005	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Hyla wrightorum</i>	US: Arizona	N	2	Bait use	Early 1960s	Stebbins, 1966; Vitt & Ohmart, 1978	
hylid sp.	New Zealand US: Indiana	N N	1 2	Cargo stowaway Cargo stowaway (2)		Gill et al., 2001 Minton, 1972	
<i>Hymenochirus boettgeri</i>	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966	
<i>Hymenochirus curtipes</i>	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Hypsibous albomarginatus</i> (syn: <i>Hyla albomarginata</i>)	Great Britain	N	15	Cargo stowaway (15)	1960s (15)	Yalden, 1965	
<i>Kaloula picta</i>	Guam	N	1	Cargo stowaway	1990	McCoid, 1993a; Christy et al., 2007b	
<i>Kaloula pulchra</i>	Australia Guam	N N	1 1	Cargo stowaway Cargo stowaway	2005 2003	Tyler & Chapman, 2007 Christy et al., 2007a, b Parker, 1934	
	Indonesia: Sulawesi Malaysia: Sabah & Sarawak	Y Y	1 1			Matsui, 1979; Inger & Stuebing, 1997	
	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
(syn: <i>Callitula pulchra</i>)	Singapore	Y	1	Intentional	1886	Flower, 1896, 1899; Chasen, 1925; Parker, 1934; Lim & Chou, 1990; Lim & Lim, 1992	
	Taiwan	Y	1	Cargo stowaway	1990s	Lue et al., 2003	Hou et al., 2006
<i>Lechriodus fletcheri</i>	Australia	?	1	Intentional		Low, 2003	
<i>Leptodactylus fallax</i>	Grenada	N	1			Groome, 1970	
	Jamaica	N	1	Food	1967	Proctor, 1973; Crombie, 1999	
	Martinique	N	1			Lescure, 1983	

(syn: <i>Leptodactylus pentadactylus</i>)	Puerto Rico	N	3	{Biocontrol, food} (3)	1929, 1932 (2)	May, 1930; Grant, 1931, 1932a, b; Barbour, 1937; Rivero, 1978; R. Thomas & Joglear, 1996
<i>Limnodynastes dorsalis</i>	Australia	Y	1			Low, 2003
<i>Limnodynastes dumerilii</i>	New Zealand	N	1	Intentional	1999	Whitaker & Bejakovich, 2000
<i>Limnodynastes tasmaniensis</i>	Australia	Y	3	Cargo stowaway (3)	1971, 1990s (2)	Martin & Tyler, 1978; O'Dwyer et al., 2000
<i>Limnodynastes terrae-eginae</i>	Australia	N	1	Cargo stowaway	1990's	O'Dwyer et al., 2000
<i>Litoria adelaidensis</i>	Christmas Island	N	1	Cargo stowaway	1980	Hicks & Heatwole, 1980
	New Zealand	?	1		1981	B.D. Bell, 1982a, b
<i>Litoria aurea</i>	Loyalty Islands	Y	1			Bauer & Vindum, 1990; Bauer & Sadlier, 2000
(syn: <i>Hyla aurea</i>)	New Caledonia	Y	1	Cargo stowaway	1800s	Roux, 1913; Sarasin, 1925; Copland, 1957; J.A. Moore, 1961; Neill, 1964; Bauer & Vindum, 1990; Gargominy et al., 1996; Bauer & Sadlier, 2000
(syn: <i>Hyla aurea</i>)	New Zealand	Y	1	Biocontrol	1867	Thomson, 1922; Archey, 1935; Falla, 1957; McCann, 1961; Robb, 1973, 1986; West, 1979; B.D. Bell, 1982a, b; Gill, 1986; Gill & Whitaker, 1996; Gill et al., 2001; Lever, 2003
	US: Hawaii	N	1	Biocontrol	1929	E.H. Bryan, 1932; Tinker, 1938

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Vanuatu	Y	1	Biocontrol	1967	Medway & Marshall, 1975; Tyler, 1979	
	Wallis Island	Y	1	Biocontrol	1930	Eldredge, 1994, 2000; Bauer et al., 1997	
<i>Litoria bicolor</i>	Australia	N	13	Cargo stowaway (13)	1975 (4), 1976 (6), 1979 (2), 1990s	Tyler, 1982; O'Dwyer et al., 2000	
<i>Litoria caerulea</i>	Australia	N	8	Cargo stowaway (6)	1977, 1979, 1990s (5)	Tyler, 1982; Limpus et al., 1999; Gillespie & Clemann, 2000; O'Dwyer et al., 2000	
	Australia: Norfolk Island	N	3	Cargo stowaway (2)	1998 (2), 1999	Covacevich et al., 2001	
(syn: <i>Hyla caerulea</i> , <i>Hyla caerulea</i>)	New Zealand	N	12	Biocontrol (10), cargo stowaway (2)	1897 (8), 1899 (2)	Thomson, 1922; Archey, 1935; Fällä, 1957; McCann, 1961; Sharell, 1966; Robb, 1973, 1986; West, 1979; B.D. Bell, 1982a, b; Tyler, 1982; Gill et al., 2001	Barwick, 1961
	US: Florida	?	2	Pet trade (2)	1990	Bartlett, 1994a; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2004a	
<i>Litoria chloris</i>	Australia	?	2	Cargo stowaway, intentional	1990s (2)	O'Dwyer et al., 2000; Low, 2003	
<i>Litoria cyclorhyncha</i>	Australia	Y	1			Low, 2003	

<i>Litoria ewingii</i>	Australia	N	1	Cargo stowaway	1998	O'Dwyer et al., 2000
	Australia: Lord Howe Island	Y	1	Cargo stowaway		Low, 2003
	Great Britain	N	1	Intentional	1951	Larking, 1955; Fitter, 1959; R.H.R. Taylor, 1963; J.F.D. Frazer, 1964
(syn: <i>Hyla ewingii</i>)						
(syn: <i>Hyla ewingii</i> , <i>var. calliscelsis</i>)	New Zealand	Y	1	Biocontrol	1875	Marriner, 1907; Thomson, 1922; Archev, 1935; Falla, 1957; McCann, 1961; Sharell, 1966; Gill, 1973, 1978, 1986; Robb, 1973, 1986; West, 1979; B.D. Bell, 1982a, b; B.W. Thomas, 1982; Gill & Whitaker, 1996
<i>Litoria fallax</i>	Australia	N	4	Cargo stowaway (3)	1975, 1990s (3)	Tyler, 1982; Gillespie & Clemann, 2000; O'Dwyer et al., 2000
	CNMI	N	1			Rodda et al., 1991; McCoid, 1999; S.R. Vogt & Williams, 2004
	Guam	Y	1		1968	Falanruw, 1976; Tyler, 1982; Eldredge, 1988, 1994, 2000; McCoid, 1993a, 1999; Christy et al., 2007b
<i>Litoria gracilentia</i>	Australia	N	13	Cargo stowaway (13)	1975 (4), 1976, 1998 (5), 1990s (3)	Tyler, 1982; K. Griffiths, 1997; O'Dwyer et al., 2000

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	New Zealand	N	2	Cargo stowaway (2)	1972	B.D. Bell, 1982a, b; Gill et al., 2001	
<i>Litoria infrafrenata</i>	Australia	N	15	Cargo stowaway (15)	1975 (5), 1976 (5), 1977, 1979 (2), 1990s (2)	Tyler, 1982; O'Dwyer et al., 2000	
(syn: <i>Hyla dolichopsis</i> , Indonesia; Java <i>Hyla trimilensis</i>)		N	1	Nursery trade		van Kampen, 1907; Tyler, 1968, 1982	
<i>Litoria phyllocroa</i>	Australia	N	1	Cargo stowaway	1976	Tyler, 1982	
<i>Litoria raniformis</i> (syn: <i>Hyla aurea</i>)	New Zealand	Y	3	{Biocontrol, duck food}	1867, 1868 (2)	Hutton, 1904; Mairiner, 1907; Thomson, 1922; Copland, 1957; McCann, 1961; J.A. Moore, 1961; Sharell, 1966; Robb, 1973, 1986; West, 1979; B.D. Bell, 1982a, b; B.W. Thomas, 1982; Gill & Whitaker, 1996	Cree, 1984, 1985; Fordham, 1985; Ford, 1989; P.J. Bishop, 1999; McKenna, 2001; Waldman et al., 2001
<i>Litoria rothii</i>	Australia	N	1	Cargo stowaway	1975	Tyler, 1982	
	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Litoria rubella</i>	Australia	N	4	Cargo stowaway (4)	1975, 1977, 1990s (2)	Tyler, 1982; O'Dwyer et al., 2000	
<i>Litoria verreauxii</i>	Australia	N	1	Cargo stowaway	1998	O'Dwyer et al., 2000	
<i>Litoria xanthomera</i>	Australia	N	1	Cargo stowaway	1998	O'Dwyer et al., 2000	

<i>Litoria</i> sp.	New Zealand	N	2	Nursery trade (2)	1977	Gill et al., 2001 Ota, 1983, 1995, 1999; Toyama, 1984a; Chigira, 1988; Toyama & Ota, 1991; Hikida et al., 1992; Ota et al., 1994a, 2004a; Goris & Maeda, 2004; Toda & Yoshida, 2005
	Japan: Ryukyu Islands	Y	1			
<i>Microhyla ornata</i>						
<i>Microhyla pulchra</i>	Guam	?	1	Aquaculture con- taminant	2004	Christy et al., 2007a, b
<i>Osteopilus septentri- onalis</i>	Anguilla	Y	2	Nursery trade (2)	1980s, 1999	Townsend et al., 2000; Hodge et al., 2003
	Antigua	Y	1	Nursery trade	1990s	Dalry, 2007
	Bahamas: Great Inagua	Y	1		1960s	Schwartz, 1968b
	Bonaire British Virgin Islands	Y Y	1 3	Nursery trade Cargo stowaway (2), nursery trade	2002 1990, 1993, 2000	van Buurt, 2005 Meshaka, 1996a; Lever, 2003; J. Owen et al., 2005a, 2006; Perry & Gerber, 2006; Perry et al., 2006
Canada: Ontario		N	3	Nursery trade		Meshaka, 1996a
	Costa Rica	Y	1	Cargo stowaway	Mid-1980s	Duellman, 2001; Savage, 2002
Curaçao Dominica		N	1	Nursery trade	2000	van Buurt, 2005
		N	1	[Cargo stowaway, nursery trade]	2006	Malhotra et al., 2007 van Buurt, 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Nevis	Y	1	Nursery trade	1950s	Lever, 2003	
	Puerto Rico	Y	1			Duellman & Crombie, 1970; Rivero, 1978; Joglar & Rios-L., 1995; R. Thomas & Joglar, 1996; Joglar et al., 1998	Vargas-Salinas, 2006a-c
	Saba	?	1		2006	Powell, 2006, 2007	
	St. Barts	Y	2	Nursery trade (2)	1995, 1996	Breuil, 2002; Hodge et al., 2003	
	St. Maarten	Y	1	Nursery trade	~1987	Powell et al., 1992, 2005; H. Kaiser & Henderson, 1994; Townsend et al., 2000; Breuil, 2002; Hodge et al., 2003	
	U.S. Virgin Islands	Y	2	Intentional, nursery trade	1974	Schwartz & Thomas, 1975; Philibosian & Yntema, 1976, 1977; MacLean, 1982; Waddle et al., 2005; Platenberg & Boulon, 2006	
	US: Colorado	N	1	Nursery trade	1989	Livo et al., 1998	

(syn: <i>Hyla dominicensis</i> , <i>Hyla septentrionalis</i>)	Y	1	[Cargo stowaway, 1800s nursery trade]	<p>Barbour, 1931b, 1937; Stejneger & Barbour, 1933; Carr, 1940; Allen & Slatten, 1945; Trapido, 1947; A.H. Wright & Wright, 1949; Mittleman, 1950; Schwartz, 1952; Allen & Neill, 1953; W. King, 1960; W. King & Krakauer, 1966; Duellman & Crombie, 1970; D.F. Austin, 1973; Ashton, 1976; H.M. Stevenson, 1976; Layne et al., 1977; S. Myers, 1977; Wilson & Porras, 1983; Lazell, 1989a; Somma & Crawford, 1993; Meshaka, 1996a, 2005; Butterfield et al., 1997; Bartlett & Bartlett, 1999; T. Campbell, 1999b; Krysko & King, 1999; Christman et al., 2000; Meshaka et al., 2000, 2004a; Dodd & Griffey, 2002; Townsend et al., 2002; S.A. Johnson et al., 2003b; Johnston, 2004; S.A. Johnson, 2004; Welker, 2004; Krysko et al., 2005</p>	<p>Peterson et al., 1952; Duellman & Schwartz, 1958; D.S. Lee, 1968, 1969; Steiner, 1983; Crump, 1986; Dalrymple, 1988; Meshaka, 1993, 1996b-g, 2001; Dalrymple, 1994; Love, 1995; Meshaka & Ferster, 1995; Meshaka & Jansen, 1997; Babbitt & Meshaka, 2000; Nelson et al., 2002; Maskell et al., 2003; K.G. Smith, 2004, 2005a, b; Wyatt & Forsy, 2004; McKie et al., 2005; Guzy et al., 2006; Pieterse et al., 2006; Bartareau & Meshaka, 2007; T.S. Campbell, 2007</p>
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Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Georgia	?	1		2004	S.A. Johnson, 2007	
	US: Hawaii	?	1	Pet trade	Early 1980s	McKeown, 1996	
	US: Maryland	N	3	Cargo stowaway (3)	1927	Mansueti, 1941a; Meshaka, 1996a	
	US: Virginia	N	1	Nursery trade	1992	Mitchell, 1999	
<i>Rachymedusa dae nicolor</i>	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966	
<i>Pelobates fuscus</i>	Great Britain	N	1			Nöllert, 1997	
	Malta	N	1	Intentional	1910s	Despott, 1913	
<i>Phrynohyas venulosus</i>	US: Kentucky	N	1	Cargo stowaway	1928	W.R. Allen, 1928	
<i>Phrynomantis bifasciatus</i> (syn: <i>Phrynomerus bifasciatus</i>)	South Africa	N	1	Cargo stowaway		Stegfried, 1962; Bruton & van As, 1986; de Moor & Bruton, 1988	
<i>Physalaemus pustulosus</i>	Costa Rica	Y	3		2001(2)	Savage, 2002; Ryan, 2007	
<i>Pipa carvalhoi</i>	Brazil	Y	1			C. Lever, 2003	
<i>Pipa parva</i>	Venezuela	Y	1	Pet trade	~1990	Royero & Hernández, 1995; Measey & Royero, 2005	
	Bonaire	Y	1	Intentional	1928	van Buurt, 2005	van Wijngaarden, 1988
	Curaçao	Y	1	Cargo stowaway	1910	van Buurt, 2005	
	Klein Bonaire	Y	1			van Buurt, 2005	
<i>Polypedates leucomystax</i>	Guam	N	1	Cargo stowaway	1993	Wiles, 2000; Christy et al., 2007b	
	Indonesia: West Papua	Y	1			Iskandar, 1998	

Japan: Ryukyu Islands	Y	1	Cargo stowaway	1964	Utsonomiya, 1977; Chigira, 1984; Toyama, 1984a, b; Moriguchi, 1988; Maeda & Matsui, 1989; Toyama & Ota, 1991; Masunaga, 1993; Ota, 1995, 1999, 2000, 2002c; Iwanaga, 1998; Nohina et al., 1998; Nakata, 2001; Kawauchi, 2002; Yoshigou et al., 2003; Goris & Maeda, 2004; Ota et al., 2004a; Shiroma & Ota, 2004; Toda & Yoshida, 2005	H. Hasegawa, 1989, 1993; Tanaka, 1995
<i>Polypedates megacephalus</i>	Y	1	Aquaculture contaminant	2004	Christy et al., 2007a, b	
<i>Pseudacris clarkii</i>	N	1	Aquaculture contaminant	1998	Shepard & Burdett, 2000	
<i>Pseudacris crucifer</i> (syn: <i>Hyla crucifer</i>)	N	1			Schwartz & Thomas, 1975; Schwartz & Henderson, 1988, 1991; Estrada & Ruibal, 1999	
<i>Pseudacris regilla</i>	Y	2	Intentional (2)	1933, 1961–1962	Stebbins, 1985; Reimchen, 1990; Waters, 1992; Rorabaugh & Lannoo, 2005	
	?	2	Pet trade (2)	1984, 1985	Eckstein & Meimig, 1989	
(syn: <i>Hyla regilla</i>)	N	1	Intentional		J.F.D. Frazer, 1964	
	N	2	Cargo stowaway (2)	1989, 2005	McCoid, 1993a; Christy et al., 2007a, b	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Alaska	Y	1	Intentional	1960	Waters, 1992; Waters et al., 1998	
	US: Arizona	Y	4	Intentional, nursery trade (3)	1980, 2001	Howland, 1996; Rorabaugh et al., 2004; Rorabaugh & Lannoo, 2005	
	US: California	Y	2			Stebbins, 1985	
	US: Colorado	N	2	Nursery trade (2)	Early 1980s, 1994	Livo et al., 1998	
<i>Pseudacris triseriata</i>	Canada: Newfoundland	N	3	Biocontrol	1963 (3)	Buckle, 1971; Maunder, 1983, 1997; F.R. Cook, 1984; C.E. Campbell et al., 2004	
<i>Pyxicephalus adspersus</i>	Belgium	N	3	Pet trade (3)		Jooris, 2000	
	Egypt	?	1	Cargo stowaway	1990s	Ibrahim, 2001c; Baha el Din, 2006	
	Mauritius	Y	2		1769, 1792	Mertens, 1934; Cheke, 1987; Tonge, 1990; Vences et al., 2004a	
	Réunion	Y	1		1830s	Maillard, 1862; Bour & Moutou, 1982; Cheke, 1987; Vences et al., 2004a	
(syn: <i>Rana mas-careniensis</i>)	Seychelles	Y	1			Mertens, 1934; Vesey-FitzGerald, 1947; Honegger, 1966; Vences et al., 2004a	
<i>Pyxicephalus adspersus</i>	South Africa	?	1	Intentional		de Moor & Bruton, 1988	

<i>Rana aurova</i> <i>Rana bedriagae</i> (syn: <i>Rana ridibunda</i>)	US: Alaska	Y	1	Intentional	1982	Hodge, 2004
	France	?	6	Food (6)		Pagano et al., 2003; Pascal et al., 2006
<i>Rana bergeri</i> <i>Rana berlandieri</i>	Malta	Y	1		Late 1990s	Sciberras & Schembri, 2006a, b
	Great Britain	Y	1			Wycherley et al., 2003
	Mexico	Y	2	Spread from adjacent introduction (2)		Rorabaugh et al., 2002; Rorabaugh & Servoss, 2006
<i>Rana catesbeiana</i> (syn: <i>Lithobates catesbeianus</i>)	US: Arizona	Y	1	Aquaculture contaminant	1960s	Clarkson & Rorabaugh, 1989; Platz et al., 1990; Platz, 1991; Jennings & Hayes, 1994; Rorabaugh et al., 2002; Brennan & Holycross, 2005; Rorabaugh, 2005
	US: California	Y	1	Aquaculture contaminant	1960s	Clarkson & Rorabaugh, 1989; Platz et al., 1990; Platz, 1991; Jennings & Hayes, 1994; Rorabaugh et al., 2002; Jennings, 2004; Jennings & Fuller, 2004; Rorabaugh, 2005
<i>Rana blairi</i> <i>Rana catesbeiana</i> (syn: <i>Lithobates catesbeianus</i>)	US: Utah	Y	1	Spread from adjacent introduction		Rorabaugh et al., 2002
	US: Colorado	N	1	Bait use	1950	Livo et al., 1998
	Argentina	Y	4	Food (1)		Welcomme, 1988; Rueda-Almonacid, 1999; Pereyra et al., 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Austria	N	1		1927	C.R. Boettger, 1941; Veenvlriet & Veenvlriet, 2002	
	Belgium	Y	12	Pet trade (6)	1980s (2), 1990s (2)	Stumpel, 1992; Schops, 1999; Jooris, 2002; Percsy & Percsy, 2002a; Veenvlriet & Veenvlriet, 2002; Duguet & Melki, 2003; Ficetola et al., 2007b	
	Brazil	Y	2	Food (2)	1935, mid-1980s	Bury & Whelan, 1984; Welcomme, 1988; Guix, 1990; Kwet, 1999; Rueda-Almonacid, 1999; Borges-Martins et al., 2002	F.L. de Souza et al., 1993; Bernarde & Machado, 2001; Batista, 2002; Souza et al., 2003; Garner et al., 2006; da Silva et al., 2007; Dos Reis et al., 2007
	Canada: British Columbia	Y	2	Food (2)	1930s (2)	Carl, 1949; Dumas, 1966; Carl & Guiguet, 1972; Green, 1978; F.R. Cook, 1984; Orchard, 2000	Green, 1978; Pearl et al., 2005b; Garner et al., 2006; Govindarajulu et al., 2005, 2006; Govindarajulu & Anholt, 2006
	Canary Islands	?	1			Pleguezuelos, 2004	
	Chile	Y	1	Food		Lever, 2003	
	China	Y	2	Food (2)	1960s	Tan & Tong, 1989; Ye et al., 1993; Zhao & Adler, 1993; Fei, 1999; Fei & Ye, 2000; Z. Li & Xie, 2002; C. Li & Xie, 2004; Wu et al., 2004	He, 1998; Wu et al., 2005; Zhou et al., 2005; Y. Li et al., 2006; Wang et al., 2006, 2007

Colombia	Y	1	Food	1986	J. Baker, 1995; Rueda-Almonacid, 1998, 1999; Acosta-Galvis, 2000; Barrio Amorós 2001; Lever, 2003	Daza-Yaca & Castro-Herrera, 1999
Cuba	Y	1	Food	1915	Hoffman & Noble, 1927; Martínez, 1948; Neill, 1964; Jaume, 1966; Buidé, 1967; G. Peters, 1974; Garrido & Jaume, 1984; de Armas et al., 1987; Novo Rodríguez et al., 1988; Escobar Herrera, 1995; Estrada & Ruibal, 1999	Odening, 1968; Martínez et al., 1982; Coy Otero & Ventosa, 1984; Sampetro Marín et al., 1985, 1986; Coy Otero & Martínez, 1987; Sampetro Marín & Montañez Huguez, 1993; Montañez et al., 1996
Denmark	N	2	Pet trade (2)	1990s (2)	Fog et al., 1997; Veenvliet & Veenvliet, 2002	
Dominican Republic	Y	1	Food	1955	Schwartz & Thomas, 1975; Garrido & Jaume, 1984; Welcomme, 1988; Schwartz & Henderson, 1991; Powell et al., 1999	
Ecuador	Y	1	Food	Late 1990s	J. Baker, 1995; Lever, 2003; Cisneros-Heredia, 2004	
France	Y	6	Food (2), pet trade (3)	Late 1800s (2), 1968, 1981, 1990, 2002	Dubois, 1983; Touratier, 1992a, b; Haffner, 1997; Lanza & Ferri, 1997; Neveu, 1997; Jooris, 2000; Veenvliet & Veenvliet, 2002; Duguet & Melki, 2003; Pascal et al., 2006; Ficotola et al., 2007b	Detaint and Coïc, 2006; Garner et al., 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Germany	Y	17	Biocontrol (1), food (3), pet trade (13)	1911, 1927, 1934, 1978 (2), 1980 (3), 1985–1990 (2), 1987, 1988, 1990 (3), 1992, early 1990s	C.R. Boettger, 1941; Geiger & Niekisch, 1983; Honegger, 1984; Eckstein & Meinig, 1989; Münch, 1992; Nöllert & Nöllert, 1992; Stumpel, 1992; Thiesmeier et al., 1994; Bammerlin & Bitz, 1996; Geiger & Waitzmann, 1996; Dalbeck et al., 1997; Schlippmann & Geiger, 1998; Laufér & Waitzmann, 2002; Veenvliet & Veenvliet, 2002; Ficetola et al., 2007b	Laufer, 2004; Laufer & Sandte, 2004
(syn: <i>Rana cates- byana</i>)	Great Britain	N	3	Intentional, pet trade (2)	1905, 1996	Swanton, 1928; Fitter, 1959; J.F.D. Frazer, 1964; Banks et al., 2000; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002; Veenvliet & Veenvliet, 2002; Lever, 2003; Ficetola et al., 2007b	Cunningham et al., 2005; Garner et al., 2006; M.C. Fisher & Gamer, 2007
	Greece: Crete	Y	1	Food	1997	Veenvliet & Veenvliet, 2002; Ficetola et al., 2007b	

Guyana	Y	1		Rueda-Almonacid, 1999	
Haiti	Y	1	Food	Powell et al., 1999	Neils & Bugbee, 2007
Indonesia	Y	1	Food	Eidman, 1989; Iskandar, 1998; McKay, 2006	
Israel	Y	1		Anonymous, 1995; Rueda-Almonacid, 1999	
Italy	Y	5	Food (2)	1935, mid-1930s, Capocaccia, 1957; Lanza, 1962, 1983b; Tortonese & Lanza, 1968; Albertini, 1970a, b, 1972, 1983; Bennati et al., 1975; Bruno, 1978; Vanni & Lanza, 1978, 1982; Andreone et al., 1987; Albertini & Lanza, 1988; Salmaso & Oselta, 1989; J. Baker, 1995; Lanza & Corti, 1993, 1996; Mazzotti & Stagni, 1993; Lapini et al., 1996, 1999; Societas Herpetologica Italica, 1996; Viora, 1996; Lanza & Ferri, 1997; Andreone & Marocco, 1998; Bertolino, 1999; Bologna et al., 2000; Veenfliet & Veenfliet, 2002; Ficetola et al., 2007b	Bagnoli & Albertini, 1984; Touratier, 1992b; Picatello, 1993; Garner et al., 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Jamataca	Y	3	Food (2)	1967	C. Grant, 1946; Proctor, 1973; Mahon & Aiken, 1977	
	Japan: Izu Islands	Y	1	Food	1952	Goris, 1967; Ota, 2002b	A. Uchida, 1975, 1976; A.
	Japan: mainland	Y	2	Food (2)	1920s (2)	Kaburaki, 1933; Maeda & Matsui, 1989; Matsui, 1990; M. Hasegawa, 1999; Ota, 1999, 2000, 2002b; Hongo, 2000; Uchiyama et al., 2002; Toda & Yoshida, 2005	Uchida & Itagaki, 1980; Yoneyama & Iwasawa, 1985; Oyamada et al., 1998; Khonsue & Matsui, 2001; Manunouchi et al., 2003; H. Hasegawa & Asakawa, 2004; Hirai, 2004; Yoshikawa et al., 2004; Garner et al., 2006; H. Hasegawa, 2006; Hirai, 2006a, b
	Japan: Ogasawara Islands	Y	1			Toda & Yoshida, 2005	
	Japan: Ryukyu Islands	Y	8	Food (8)	1953 (5), 1954 (2), late 1950s	Ota, 1983, 1986a, 1995, 1999, 2000, 2002b; Honegger, 1984; Toyama, 1984a; Toyama & Ota, 1991; Takahashi & Miyahara, 1998; Levet, 2003; Toda et al., 2003; Goris & Maeda, 2004; Ota et al., 2004a; Tanaka, 2004	Otani, 1987
	Malaysia	?	1			Anonymous, 1995	

Mexico	Y	2	Food (2)	1945, 1970	H.M. Smith & Taylor, 1948; Stebbins, 1951; Hardy & McDiarmid, 1969; Funk & Croulet, 1976; Mullen, 1976; Conant, 1978; Arredondo-Figueroa, 1983; Stebbins, 1985; W.W. Tanner, 1989; Grismer & McGuire, 1993; J. Baker, 1995; Lemos-Espinal et al., 2000; McPeak, 2000; Casas-Andreu et al., 2002a, b; Grismer, 2002a; Domínguez-Torres & Mellink, 2003	Conant, 1978
Namibia	Y	1			Rueda-Almonacid, 1999	
Netherlands	N	47	Aquaculture contaminant, pet trade	1986	de Graaf, 1990; Smit & Zuidervijk, 1990a; Melchers & Timmermans, 1991; Stumpel, 1991, 1992; Muddle, 1992; Timmermans, 1993; Veenvliet, 1996; Lanza & Ferri, 1997; Schops, 1999; Sneeep, 1999; Jooris, 2000; Veenvliet & Veenvliet, 2002; Fietola et al., 2007b	Breuls, 1993
Peru	Y	1			Anonymous, 1995; Rueda-Almonacid, 1999	
Puerto Rico	Y	1	Food	1935	Perez, 1951; Philibosian & Yntema, 1977; Rivero, 1978; R. Thomas & Joglear, 1996; Joglear, 1998	Perez, 1951; López-Flores et al., 2003

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Russia	Y	1			Rueda-Almonacid, 1999	
	Singapore	?	1	Food	1980s	Lim & Lim, 1992; Ng et al., 1993	
	South Korea	Y	1			Kim & Ko, 1998	Kim et al., 1992; Jeong et al., 2002a, b
	Spain	N	3	Food (2)	1980s, 2000	García-París, 1991; Rivera & Arribas, 1993; Arano et al., 1995; Mateo, 1997a; Ayllón, 1999a; Veenvliet & Veenvliet, 2002; García-París et al., 2004; Pleguezuelos, 2004; Ficetola et al., 2007b	Ayllón, 1999b
	Sri Lanka	Y	1			Rueda-Almonacid, 1999	
	Tadjikistan	Y	1			Anonymous, 1995; Rueda-Almonacid, 1999	
	Taiwan	Y	2	Food (2)	1924, 1951	Leviton, 1971; Liao & Liu, 1989; J. Baker, 1995; Ota, 2000; Lue et al., 2003	Hou et al., 2006
	US: Arizona	Y	1			K.P. Schmidt, 1924; Dill, 1944; A.H. Wright & Wright, 1949; K.B. Jones et al., 1982; Bury & Whelan, 1984; Clarkon & Rorabaugh, 1989; Rosen et al., 1995; Brennan & Holycross, 2005; Casper & Hendricks, 2005; Lazaroff et al., 2006	Clarkson & deVos, 1986; Schwalbe & Rosen, 1988; Jennings & Hayes, 1994; Rosen & Schwalbe, 1995; 1996a, b, 2002; Rosen et al., 1995; Goldberg et al., 1998b; K.A. King et al., 2002; León-Régagnon et al., 2005; Garner et al., 2006; Kahrs, 2006; Maret et al., 2006; Servoss & Sharrocks, 2006

US: California Y 6 Food (5), lab release

1896, 1910s, 1912 (2), 1914, 1915

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(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
(syn: <i>Rana cates-beana</i>)							
	US: Colorado	Y	3	Food (2)	1913, 1914	Ellis & Henderson, 1915; Maslin, 1950, 1959; Hammerson, 1982, 1999; Norris et al., 1994; Chiszar et al., 1995; Rybak et al., 1995; Livo et al., 1998; Casper & Hendricks, 2005	Buhler, 1970; Hammerson, 1982; Kmiecik, 2004
	US: Hawaii	Y	2	Biocontrol, food	1897–1899, 1902	Jordan & Evermann, 1905; W.A. Bryan, 1915; Storer, 1925; E.H. Bryan, 1932; Tinker, 1938; Oliver & Shaw, 1953; Hunsaker & Brese, 1967; Jennings & Hayes, 1985; McKeown, 1996	Mercalf, 1923; Ingles, 1933; La Rivers, 1948; Baldwin et al., 1952; Viernes, 1995
	US: Idaho	Y	1		1890	Van Denburgh & Slevin, 1921; Erwin, 1928; J.R. Slater, 1941; Dumas, 1966; Nussbaum et al., 1983; Casper & Hendricks, 2005	Waiz, 1961, 1962; Murray et al., 2004; Morello et al., 2006
	US: Iowa	Y	1	Food (2)	1930s, 1960s	Christiansen & Bailey, 1991; Lannoo et al., 1994; Christiansen, 2001; Casper & Hendricks, 2005	
	US: Kansas	Y	1			Bury & Whelan, 1984; Sparks et al., 1999; Casper & Hendricks, 2005	

US: Massachusetts	N	2		Cardoza et al., 1993
US: Minnesota	Y	1		Oldfield & Moriarty, 1994; Casper & Hendricks, 2005
US: Montana	Y	1	1920	Black & Bragg, 1968; Black, 1969; Casper & Hendricks, 2005
US: Nebraska	Y	1	Food	Hudson, 1942; Bury & Whelan, 1984; Casper & Hendricks, 2005
US: Nevada	Y	5	1920, 1934, 1935, 1936, 1938	Linsdale, 1940; La Rivers, 1942; Stebbins, 1951; Banta, 1965; Jennings & Hayes, 1994; Casper & Hendricks, 2005
US: New Mexico	Y	1	1885	A.H. Wright & Wright, 1949; Degenhardt et al., 1996; Casper & Hendricks, 2005
US: North Dakota	N	1		Wheeler, 1947; Wheeler & Wheeler, 1966
US: Oklahoma	Y	1		Bury & Whelan, 1984; Casper & Hendricks, 2005
US: Oregon	Y	1	1931	Jewett, 1936; Gordon, 1939; Dumas, 1966; Nussbaum et al., 1983; Casper & Hendricks, 2005

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
							Kiesecker et al., 2001; Blaustein & Kiesecker, 2002; Adams et al., 2003; Pearl et al., 2003, 2004, 2005a, b, 2006; Blaustein et al., 2005; Pearl & Green, 2005; Rombough & Schwab, 2006
	US: South Dakota	Y	1			Fishbeck & Underhill, 1960; H.M. Smith et al., 1966; Bury & Whelan, 1984; Casper & Hendricks, 2005	
	US: Texas	Y	3	Food	1927	Neck, 1980, 1983; Bury & Whelan, 1984; Killebrew et al., 1995; Manning et al., 1995; Dixon, 1987, 2000; Pendley, 2001; Casper & Hendricks, 2005	
	US: Utah	Y	1			Stebbins, 1951; Dumas, 1966; Bury & Whelan, 1984; Casper & Hendricks, 2005	
	US: Washington	Y	3	Food	1910	Svihla & Svihla, 1933; W.C. Brown & Slater, 1939; J.R. Slater, 1939, 1955; Dumas, 1966; Nussbaum et al., 1983; K.R. McAllister, 1995; Casper & Hendricks, 2005	Lardie, 1963; D.L. Lehmann, 1964; Richter & Azous, 1995; Adams et al., 1998; Adams, 1999, 2000; Pearl et al., 2005b

US: Wyoming	Y	2				Baxter & Stone, 1980; Koch & Peterson, 1995; Casper & Hendricks, 2005
Venezuela	Y	1	1990s			Barrio Amorós, 2001, 2002; Díaz de Pascual & Chacón Ortiz, 2002; Hanselmann et al., 2004
<i>Rana clamitans</i>						
Bahamas	?	1	2001			D.S. Lee, 2004, 2005
Canada: British Columbia	Y	2	1940s	Pet trade (2)		Carl, 1949; Carl & Guiguet, 1972; M. Stewart, 1983; F.R. Cook, 1984
Canada: Newfoundland	Y	2	1860 (2)	Intentional (2)		Maret, 1867; C. Hardy, 1869; Johansen, 1926; Bleakney, 1954; Cameron & Tomlinson, 1962; Maunder, 1983, 1997; M. Stewart, 1983; F.R. Cook, 1984; C.E. Campbell et al., 2004
Netherlands	N	1	1983			Gubbels, 1992
US: Arizona	?	1				Howland, 1996
US: Iowa	Y	1				Pauley & Lannoo, 2005
US: Montana	?	1				Stebbins, 1985
US: Utah	Y	1	1940s	Pet trade		Behle & Erwin, 1962
US: Washington	Y	1	1910			J.R. Slater, 1939, 1955; Stewart, 1983; Nussbaum et al., 1983; K.R. McAllister, 1995
<i>Rana dalmatina</i>	N	1				Parent, 1983

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Rana draytonii</i> (syn: <i>Rana aurora. Rana aurora draytonii</i>)	US: California	Y	3	Food (3)	Mid-1910s	Storer, 1933a; Jennings, 1988a; Fellers, 2005	
(syn: <i>Rana aurora, Rana aurora draytonii</i>)	US: Nevada	Y	2	Food (2)	1930s, 1940s	Linsdale, 1938, 1940; Stebbins, 1951, 1985; Banta, 1965; Green, 1985; Reaser, 2003; Fellers, 2005	
<i>Rana esculenta</i>	Great Britain	Y	30	Intentional, pet trade	1837 (3), 1840, 1841, 1842, 1882, 1884 (3), 1885, 1892, 1894, 1895, 1905–10, 1907, late 1920s, 1930, 1938, 1939, 1959, 1961, 1965, 1967 (2), 1977, 1979 (2)	Boulenger, 1884b, 1898; Dalglish, 1904; Fishwick, 1904; Gadaw, 1904; Russell, 1904; Swanton, 1928; Rintoul & Baxter, 1935; R.H.R. Taylor, 1948, 1963; M. Smith, 1949b, 1951a; Bunting, 1950; Fitter, 1959; J.F. Burton, 1962; J.F.D. Frazer, 1964; Yalden, 1965; Leutscher, 1971, 1975; Buckley, 1974, 1986; C. Lever, 1977, 1980; Arnold & Burton, 1978; Walters, 1981; C.A. Snell, 1983; Gillett, 1988; D. Frazer, 1989; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002; Wycherley, 2003; Wycherley et al., 2003	C.A. Snell, 1984; Wycherley & Beebee, 2003

	Malta	N	1	Intentional	1910s	Despott, 1913
	New Zealand	N	1	Duck food	1867	Thomson, 1922; West, 1979; Robb, 1986
<i>Rana graeca</i>	Spain	Y	4	Food (1)	Late 1980s (1)	Arano et al., 1995
<i>Rana grafi</i>	Belgium	N	1			Parent, 1983
<i>Rana grylio</i>	Belgium	Y	1	Food	1990s	Percy & Percy, 2002b
	Bahamas	Y	2		1950s	Neill, 1964; Schwartz, 1968b; D.G. Campbell, 1978; Schwartz & Henderson, 1991; Franz et al., 1996; D.S. Lee, 2004, 2005
	China	?	1			Ye et al., 1993; Fei, 1999; Fei & Ye, 2000; Li & Xei, 2004
	Puerto Rico	Y	1		Early 1990s	Rios-López & Jøglar, 1999, 2000
<i>Rana guentheri</i>	Guam	Y	1	Aquaculture contaminant	2001	Christy et al., 2007a, b
<i>Rana hecksheri</i>	China	?	1			Ye et al., 1993; Fei, 1999; Fei & Ye, 2000; Li & Xei, 2004
<i>Rana hispanica</i> (syn: <i>Rana esculenta</i>)	Italy: Sardinia	N	2	Intentional (2)	1876, 1966	Emery, 1880; Serra, 1969; Lanza & Corti, 1993, 1996
<i>Rana japonica</i>	Japan: Izu Islands	Y	1			Goris, 1967; M. Hasegawa, 1999; Goris & Maeda, 2004; Toda & Yoshida, 2005
<i>Rana kartmuelleri</i> (syn: <i>Rana balcanica</i>)	Denmark	Y	1	Lab release	Early 1980s	Sofianidou, 1997a; Jørgensen, 1999; Jensen, 2002; Lever, 2003

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
(syn: <i>Rana balcanica</i> , <i>Rana ridibunda</i>)	Italy	Y	1		1941	Lanza, 1962, 1983; Tortonese & Lanza, 1968; Capocaccia et al., 1969; Bologna, 1972; Hotz & Bruno, 1981; Ferri & Dell'Acqua, 1985; Lanza & Corti, 1993, 1996; Lapini & Zanghellini, 1995; Societas Herpetologica Italica, 1996; Soframidou, 1997a; Bertolino, 1999	
<i>Rana lessonae</i> (syn: <i>Rana esculenta</i>)	Great Britain	Y	3	Intentional (3)	1760	Wolley, 1847; T. Bell, 1859; Newton, 1859, 1876, 1877; S. H. Miller, 1874; A. Russell, 1874; S.H. Miller & Skerchby, 1878; Boulenger, 1884a, 1898; Gadow, 1904; Fitter, 1959; J.F.D. Frazer, 1964; Leutscher, 1971, 1975; N. Richards, 1975; Pickett & Townson, 1976; Arnold & Burton, 1978; Buckley, 1986; D. Frazer, 1989; C. Snell, 1994; Beebee & Griffiths, 2000; Zeisset & Beebee, 2001; Wycherley, 2003; Wycherley et al., 2003; C. Snell et al., 2005; Langton & Burton, 2006	Wycherley et al., 2001, 2002; Wycherley & Beebee, 2003

<i>Rana nigromaculata</i>	Spain	Y	1	Food	1980s	Arago et al., 1995
	Hong Kong	N	1	Food	1966	Karsten et al., 1998
	Japan: mainland	Y	2			Toda & Yoshida, 2005
	Russia	Y	1		1966	Kuzmin, 1999; Kuzmin & Maslova, 2003
	Turkmenistan	Y	1	Aquaculture contaminant	1960s	Kuzmin, 1994, 1999
	US: Hawaii	N	1		1925–1938	Tinker, 1938; Oliver & Shaw, 1953
	Azores	Y	1	Biocontrol	<1820	Morelet, 1860; Godman, 1870; Boettger, 1887; Barrois, 1896; Bertin, 1946; Chaves, 1949; Kauri, 1959; Ulfstrand, 1961; Malkmus, 1984, 1995, 1997; Ferrand de Almeida et al., 2001
	Balearic Islands	Y	1			Hemmer & Kadel, 1980; Alcover & Mayol, 1981; Salvador & Pérez Mellado, 1984; Tonge, 1986; J. Rivera & Arribas, 1993; Esteban et al., 1994; Palerm, 1997; Mayol, 2003; Pleguezuelos, 2004
	Belgium	Y	1		1991	Parent, 1997; Percsy & Percsy, 2002a

(continued)

Rana perezii (syn: *Rana esculenta*. Note that Lever (2003) included this population under both his *Rana esculenta* and *Rana perezii* accounts)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
(syn: <i>Rana esculenta</i>)	Canary Islands	Y	1	Food	<1770s	Drouët, 1861; Steindachner, 1891; Bertin, 1946; Kauri, 1959; Klemmer, 1976; Mellado, 1982; Bischoff, 1985; López-Jurado, 1991; Malkmus, 1997; Mateo, 1997a; Barbadillo et al., 1999; Pleguezuelos, 2004	Carrera-Moro et al., 1987a, b; Luis & Báez, 1987, 1990; Madrigal-Sesma et al., 1987; Nogales et al., 1989; Báez & Luis, 1994
(syn: <i>Rana esculenta</i> , <i>Rana temporaria</i> , <i>Rana viridis</i>)	Great Britain Madeira	Y	3 1	Food	1834	Wycherley et al., 2003 Hallowell, 1861; Boettger, 1887; Bertin, 1946; Sarmiento, 1948; Báez, 1993; Malkmus, 1995, 1997; Ferrand de Almeida et al., 2001	Wycherley & Beebe, 2003
<i>Rana pipiens</i>	Canada: Anticosti Island Canada: Newfoundland	Y ?	1 2	Biocontrol Biocontrol (2)	1899 1966 (2)	Johansen, 1926; Bleakney, 1958; F.R. Cook, 1984 Buckle, 1971; Maunder, 1983, 1997; F.R. Cook, 1984; C.E. Campbell et al., 2004	
	Canada: Vancouver Island Germany	Y N	1 2	Food Pet trade (2)	1930s 1980s, 1984	Green, 1978; F.R. Cook, 1984 Eckstein & Meinig, 1989; Münch, 1992	
	Great Britain South Korea U.S. Virgin Islands	N Y N	1 1 1			Beebe & Griffiths, 2000 Jeong et al., 2002a, b C. Grant, 1937	

<i>Rana porosa</i>	US: California	Y	14	Food (4), pet trade (2), lab release?	1904, 1918 (3), 1950s (2), 1961, 1963, 1965, 1969	Bryant, 1917; Storer, 1925; Banta & Morafka, 1966; Dixon, 1967; Bury & Luckenbach, 1976; Jennings, 1984, 1987a, 2004; Stebbins, 1985; Jennings & Fuller, 2004
	US: Hawaii	N	1			E.H. Bryan, 1932; Tinker, 1938
	US: Kansas	N	1	Lab release	1950	Collins, 1993
	US: Massachusetts	Y	21	Lab release (21)	1915	Lazell, 1976; Cardoza et al., 1993
	US: Nevada	Y	1	Food	1909	Bryant, 1917; Jennings, 1984
	US: Oklahoma	?	1	Lab release		Black & Sievert, 1989
	Japan: mainland	Y	1			Toda & Yoshida, 2005
	Belgium	Y	4	Pet trade (4)	1980s (4)	Parent, 1983; Burny & Parent, 1985; Percsy, 1993, 1995, 1998, 2000; Jooris, 2000; Percsy & Percsy, 2002a, b; Duguet & Melki, 2003
	Finland	N	2			Honegger, 1978; Terhivuo, 1981; Günther, 1990
	France	Y	3	Food, intentional, lab release		Neveu, 1989, 1997; Günther, 1990; Hafifner, 1997; Pagano et al., 1997, 2001a, 2001c; Duguet & Melki, 2003; Pascal et al., 2006
					Uzzell & Turner, 1983; Joly & Morand, 1994; Joly et al., 1994; Morand & Joly, 1995; Plénet et al., 1998, 2000a, b; Demongin & Martin, 1999; Pagano & Joly, 1999; Lodié & Pagano, 2000; Pagano et al., 2001c; Schmeller et al., 2001; Teplitsky et al., 2003, 2004	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
(syn: <i>Rana esculenta</i>)	Great Britain	Y	5	Biocontrol (1), intentional (3), lab release (1)	1884, 1934, 1939, 1948, 1980s	Boulenger, 1898; Dalglish, M. Smith, 1953; Beebee, 1980; 1904; E. P. Smith, 1939; R.H.R. Taylor, 1948, 1963; M. Smith, 1949b, 1951a; Bunting, 1950; Fitter, 1959; Menzies, 1962; J.F.D. Frazer, 1964; Yalden, 1965; Leutscher, 1971, 1975; J. Burton, 1973; Buckley, 1974, 1986; Coleridge, 1974; Beebee, 1977; C. Lever, 1977, 1980, 2003; D. Frazer, 1989; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002; Wycherley, 2003; Wycherley et al., 2003	M. Smith, 1953; Beebee, 1980; Zeisset & Beebee, 2003; Wycherley & Beebee, 2003; Gregory & Isaac, 2004
Italy		Y	1			Caldonazzi et al., 2002	
Kazakhstan		Y	4	Lab release (4)	1960s (4)	Kuzmin, 1994, 1999; Atakhanova & Bigaliev, 1995	
Kyrgyzstan		Y	1	Aquaculture contaminant	1960s	Kuzmin, 1994, 1999	
Russia		Y	14	Aquaculture contaminant (7), intentional (1)	1910, 1960s (3), 1969, 1970, 1970s, 1977, 1978, 1980 (2), 1981, 1988, 1990, 1990s	Günther, 1990; Kuzmin, 1994, 1999; Vershinin & Kamkina, 1999; Kuzmin & Maslova, 2003	Ivanova, 1995; Vershinin & Ivanova, 2006

	Spain	Y	1	Food	1980s	Aramo et al., 1995	
	Switzerland	Y	6	Food (5)	1920s, 1950, 1964, 1967, 1960s	Stemmler-Morath, 1950; C. Meylan, 1964; Escher et al., 1972; Blankenhorn, 1973; Berthoud & Perret-Gentil, 1976; Honegger, 1978; Hotz & Broggi, 1982; Rey et al., 1985; Grossenbacher, 1988a, b, c; A. Keller et al., 1993; Pillet, 1996; Marchesi et al., 1999; Morard et al., 2003	Blankenhorn et al., 1971; Hotz et al., 1992; Camici & Zimmerli, 1993; Hohenweg Peter, 2001; Hohenweg Peter et al., 2001, 2002; van Buskirk & Saxer, 2001; Vorburger, 2001a, b, c; Reyer et al., 2003; Vorburger & Reyer, 2003
<i>Rana rugosa</i>	Japan: Izu Islands	Y	1			M. Hasegawa, 1999; Toda & Yoshida, 2005	
	Japan: mainland	Y	2			Toda & Yoshida, 2005	
(syn: <i>Rana rugata</i>)	US: Hawaii	Y	1	Biocontrol	1895	E.H. Bryan, 1932; Svihla, 1936; Tinker, 1938; Fisher, 1948; Oliver & Shaw, 1953; Hunsaker & Brese, 1967; McKeown, 1996; Kraus, 2005	Pemberton, 1934; Gilbertson & Watermolen, 1998; Goldberg et al., 2005
<i>Rana saharica</i>	Canary Islands	Y	2			Barbadillo et al., 1999; Pleguezuelos, 2004	
<i>Rana septentrionalis</i>	Canada: Newfoundland	Y	1		1990s-2000s	Warkentin et al., 2003; C.E. Campbell et al., 2004	
<i>Rana sphenoccephala</i>	Bahamas	Y	1		1972	Jacobs, 1973b; D.S. Lee, 2004, 2005	
	US: California	Y	2	Aquaculture contaminant	1920s, 1957	Jennings, 2004; Jennings & Fuller, 2004	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Rana utricularia</i> (syn: <i>Rana utricularia</i>)	US: Connecticut	?	1	Lab release	1990 (3)	Klemens, 1991	
	US: Massachusetts	?	3		1963	Cardoza et al., 1993	
	Canada: Newfoundland	Y	1	Biocontrol		Buckle, 1971; Maunder, 1983, 1997; F.R. Cook, 1984; C.E. Campbell et al., 2004	
<i>Rana temporaria</i>	New Zealand	N	1	Cargo stowaway	1982, 1984,	Gill et al., 2001	
	US: Illinois	Y	21	Research (21)	1985, 1987 (2), 1988 (2), 1989, 1991 (13)	Thurrow, 1994	
<i>Rana temporaria</i>	US: Kansas	N	1		1942	Collins, 1993	
	Great Britain: Jersey	Y	3	Intentional (3)	1986, 1987 (2)	Young, 1987, 1988	
	Great Britain: Orkney Islands	?	5		1920s, 1980s (2)	Booth, 1984	
	Great Britain: Shetland Islands	Y	3	Cargo stowaway (1), inten- tional (2)	1895, 1920s (2)	Fitter, 1959; Booth, 1984	
	Ireland	Y	2	Intentional (2)	1696, 1699	T. Bell, 1839; Fitter, 1959; O'Rourke, 1970; Ní Lamhna, 1979; J.P.F. Wilson, 1986; D'Arcy & Hayward, 1992; Marnell, 1999; McCormick, 1999	R.M. Savage, 1935; M.M. Gibbons & McCarthy, 1983, 1984, 1986; Fairley, 1984; C.T. Griffin, 1989; Meharg et al., 1990; Korky & Webb, 1993, 1996; Marnell, 1998
Malta	N	1	Intentional	1910s	Despott, 1913		
New Zealand	N	1	Intentional	1864	Thomson, 1922; Archey, 1935; West, 1979; Robb, 1986; B.D. Bell, 1982a, b		

<i>Rana</i> sp. (<i>esculentia</i> or <i>hispanica</i>) (syn: <i>Rana esculenta</i>)	Italy (offshore islands)	N	3				Mertens, 1967; Tortonese & Lanza, 1968; Lanza & Corti, 1993, 1996
<i>Rana</i> sp. (<i>esculentia</i> or <i>hispanica</i>) (syn: <i>Rana esculenta</i>)	Italy: Sardinia	N	6	Food (2), intentional	1879, early 1930s		Corona & Fanzago, 1880; Sochurek, 1955; Serra, 1969; Bruno, 1980a; Hotz & Bruno, 1981; Auclair et al., 1983; Olioso, 1983; Lanza & Corti, 1993, 1996
<i>Rana</i> sp. (<i>psaltes</i> or <i>supranarina</i>) (syn: <i>Rana okinavana</i>)	Japan: Ryukyu Islands	N	1	{Biocontrol, research}	Early 1920s		Toyama, 1998
<i>Rana</i> sp. (presumed to be <i>R. draytonii</i>)	US: Hawaii	N	1	Biocontrol	1857		E.H. Bryan, 1932; McKeown, 1996
ranid sp.	New Zealand	N	1	Cargo stowaway			Gill et al., 2001
<i>Rhacophorus arboreus</i>	Japan: Izu Islands	Y	1				M. Hasegawa, 1999; Toda & Yoshida, 2005
<i>Rhacophorus viridis</i>	Japan: Izu Islands	Y	1				Toda & Yoshida, 2005
<i>Scinax quinquefasciatus</i>	Ecuador: Galapagos Islands	Y	5	Cargo stowaway (2)	1997–1998		H. Snell & Rea, 1999; H.L. Snell et al., 1999; H.L. Snell, 2000
	New Zealand	N	3	Cargo stowaway (3)			Gill et al., 2001
<i>Scinax ruber</i> (syn: <i>Hyla rubra</i> , <i>Olotygon rubra</i> , <i>Scinax rubra</i>)	Great Britain	N	11	Cargo stowaway (11)	1970s (11)		Banks, 1985
	Martinique	?	1		1990s		Breuil, 2002

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Puerto Rico	Y	1		1988	R. Thomas & Joglar, 1996; Rios-López, 1999, 2000	
	St. Lucia	Y	1	Cargo stowaway	<1891	Boulenger, 1891; Barbour, 1914, 1937; Corke, 1992; H. Kaiser & Henderson, 1994; Censky & Kaiser, 1999	
<i>Scinax x-signatus</i>	Guadeloupe	Y	1			Lorvelec et al., 2007	
<i>Strongylopus grayii</i> (syn: <i>Rana grayi</i>)	St. Helena	Y	1	Duck food	Early 1880s	Basilwisky, 1970; Ashmole & Ashmole, 2000	
<i>Syrnophus cysti-gnathoides</i> (syn: <i>Eleutherodactylus cystignathoides</i>)	US: Louisiana	Y	1			L.M. Hardy, 2004	
	US: Texas	Y	14	Nursery trade (8)		Mather & Dixon, 1976; Quinn, 1979; Baldauf, 1987; Brach, 1992; McCord, 1993; McGown et al., 1994; Taggart, 1997; De la Reza et al., 1998; Lutterschmidt & Thies, 1999; Malone, 1999; Collins & Hibbitts, 2001; F.J. Schmidt, 2004; McCoid, 2005a, b; Wallace, 2005; Hibbitts & Laurencio, 2006; Cotten & Fitzgerald, 2007; Hibbitts & Saenz, 2007; Sinclair et al., 2007	Hayes-Odum, 1990; C.T. McAllister & Freed, 1992

<i>Trachycephalus jordani</i>	New Zealand	N	2	Cargo stowaway (2)	1944	Gill et al., 2001
<i>Xenopus laevis</i>	Ascension Island	Y	1	Lab release	1944	Loveridge, 1959; Neill, 1964; Ashmole & Ashmole, 1997, 2000; Tinsley & McCoid, 1996
	Chile	Y	1		1973	Glade, 1988; Veloso & Navarro, 1988; Hermosilla, 1994; Tinsley & McCoid, 1996; Jaksic, 1998; Lobos, 2002; Iriarte et al., 2005; Lobos & Jaksic, 2005
	France	Y	1	Lab release	1980s	Fouquet, 2001; Duguet & Melki, 2003; Fouquet & Measey, 2006; Pascal et al., 2006
	Germany	?	1			Tinsley & McCoid, 1996
	Great Britain	Y	5	Intentional (5)	1955, 1962, 1967, 1970s, 1990s	J.F.D. Frazer, 1964; C. Lever, 1977, 1980, 2003; Tinsley & McCoid, 1996; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002
	Italy: Sicily	Y	1		1990s	Lillo et al., 2005; Razzetti & Sindaco, 2006
	Japan: mainland	Y	4			Kobayashi & Hasegawa, 2005a; Arao & Kitano, 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Mexico	Y	1			R.W. Murphy, 1983; Stebbins, 1985; Flores-Villela, 1993; McPeak, 2000; Domínguez-Torres & Mellink, 2003	
	Netherlands	?	2			Tinsley & McCoid, 1996	
	South Africa	?	1	Aquaculture contaminant		Bruton & van As, 1986	
	US: Arizona	Y	3	Intentional (3)	1960s (3)	Stebbins, 1985; Tinsley & McCoid, 1996; Crayon, 2005	
	US: California	Y	5	Lab release (1), pet trade (3)	Early 1960s, mid-1960s, 1974, 1975	St. Amant & Hoover, 1969; Mahardt & Knefler, 1972, 1973; St. Amant et al., 1973; Bury & Luckenbach, 1976; M.A. Bell, 1978; Jennings, 1987a, 2004; McCoid et al., 1993; Tinsley & McCoid, 1996; Crayon, 2005	McCoid, 1976, 1985; Avila & Frye, 1977, 1978; Frye & Avila, 1979; McCoid & Fritts, 1980a, b, 1989, 1993, 1995; Baird, 1983; Lafferty & Page, 1997; Crayon & Hothem, 1998; Ervin & Fisher, 2001; Kuperman et al., 2004; Mullin et al., 2004; Hothem et al., 2006; Ervin & Fisher, 2007
	US: Colorado	N	1	Pet trade	1990	Bacchus et al., 1993; Livo et al., 1998; Tinsley & McCoid, 1996	
	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966; Tinsley & McCoid, 1996	
	US: Massachusetts	N	1		1993	Cardoza et al., 1993; Crayon, 2005	

US: North Carolina	N	1				McCoid, 1995a; Tinsley & McCoid, 1996
US: Texas	N	1	1981			Blair et al., 1997; Crayon, 2005
US: Virginia	N	1	1970s or early 1980s	Pet trade		Zell, 1986; McCoid, 1995a; Tinsley & McCoid, 1996; Ernst et al., 1997
US: Wisconsin	N	1	1972			Tinsley & McCoid, 1996
US: Iowa	N	1	1911	Cargo stowaway		Ruthven, 1912; Christiansen, 2001
Australia	N	1				Low, 1999
Germany	?	1	1980	Pet trade		Eckstein & Meinig, 1989
Italy	N	1	2001			Trovò, 2002
New Zealand	?	1				West, 1979; Lever, 2003
US: Maryland	N	1	1935	Lab release		Mansueti, 1941a
Germany	N	1	1983-1984	Pet trade		Eckstein & Meinig, 1989
Spain	N	1		Pet trade		Pleguezuelos, 2004
US: Arizona	Y	5	Early 1950s (2)	Bait use (5)		Lowe, 1955; Espinosa et al., 2004

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: California	Y	14	Bait use (4)	1930s (2), 1940s, 1950s	Bury & Luckenbach, 1976; Mullen & Stebbins, 1978; Vitt & Ohmart, 1978; Jennings, 1987a, 2004; S.P.D. Riley et al., 2003; Fitzpatrick & Shaffer, 2004; Ervin & Burkhardt, 2006	
	US: Colorado	?	4	Bait use (4)		Livo et al., 1998	
	US: Connecticut	N	1		<1937	Babbitt, 1937; Klemens, 1993	
	US: Louisiana	?	1	Bait use		Dundee, 1988	
	US: New Mexico	Y	4	Bait use (4)		Degenhardt et al., 1996	
	US: Texas	Y	1	Bait use	<1974	R.A. Thomas, 1976; Karges, 1978	
	US: Illinois	Y	1		1970s	C.A. Phillips et al., 1999	
	Japan: mainland	?	2			Goris & Maeda, 2004	
<i>Ambystoma "nremblay"</i>	US: California	N	2	[Food, religious]	1939 (1)	Croker, 1942; G.S. Myers, 1951; Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
<i>Andrias davidianus</i>	US: Illinois	Y	1		1970s	C.A. Phillips et al., 1999	
<i>Andrias japonicus</i>	Japan: mainland	?	2			Goris & Maeda, 2004	
	US: California	N	2	[Food, religious]	1939 (1)	Croker, 1942; G.S. Myers, 1951; Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
<i>Aneides vagrans</i> (syn: <i>Aneides ferreus</i>)	Canada: British Columbia	Y	1	Cargo stowaway	1842–1906	Stebbins, 1985; Jackman, 1998	Stelmock & Harestad, 1980; Harestad & Stelmock, 1983; Gamer & Gregory, 2006
<i>Bolitoglossa rufescens</i>	US: Indiana	N	1	Cargo stowaway		Minton, 1972	
<i>Cryptobranchius alle-ganiensis</i>	US: New Jersey	N	1	Pet trade	1860	Surface, 1913; W.P. Alexander, 1927; Nickerson & Mays, 1973	

<i>Cynops pyrrhogaster</i>	Germany	?	4	Pet trade (4)	1978, 1980, 1980s (2)	Eckstein & Meimig, 1989; Münch, 1992
(syn: <i>Triturus pyrrhogaster</i>)	Spain	N	5	Pet trade		J. Rivera & Arribas, 1993; Pleguezuelos, 2004
	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966
<i>Desmognathus fuscus</i>	US: Massachusetts	N	2	Pet trade (2)	1932, 1979	Cardoza et al., 1993
	US: Kansas	N	1	Bait use	1960	Collins, 1993
	US: Michigan	Y	1			Carlson & Szuch, 2005
<i>Desmognathus quad-ramaculatus</i>	US: Georgia	Y	1	Bait use		J.B. Jensen & Waters, 1999
<i>Euproctus asper</i>	Belgium	N	1			Parent, 1983
<i>Eurycea cirrigera</i>	US: Illinois	Y	33	Research (33)	1975, 1976 (3), 1977 (2), 1978, 1979 (2), 1980, 1981, 1982, 1983 (2), 1984 (2), 1985 (2), 1986 (2), 1987 (4), 1988 (2), 1989 (2), 1990 (2), 1991 (2), 1996	Thurrow, 1997
<i>Necturus maculosus</i>	US: Connecticut	Y	2	Research, spread from adjacent introduction	1875, 1921	Babbitt, 1932; Klemens, 1993; Richmond, 2000

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Maine	Y	2	Research (2)	1939, 1940s	Crocker, 1960; Foye, 1961; DeGraaf & Rudis, 1983; Hunter et al., 1992; Mairs, 1999; Richmond, 2000	Little, 2002
	US: Massachusetts	Y	3	Research (1)		Warfel, 1936; Cardoza et al., 1993; Richmond, 2000	
	US: New Hampshire	Y	1	Spread from adjacent introduction		Richmond, 2000	
	US: Rhode Island	Y	1		1960s	Vinegar & Friedman, 1967; Richmond, 2000	
	US: Vermont	Y	1	Spread from adjacent introduction		Richmond, 2000	
<i>Notophthalmus viridescens</i>	US: California	N	4	Bait use, pet trade		Jennings, 1987a	
<i>Plethodon cinereus</i>	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966	
<i>Plethodon montanus</i> (syn: <i>Plethodon jordani</i>)	US: Illinois	Y	2	Intentional (2)		Thurrow, 1999	
	US: Virginia	Y	1	Intentional	1930s	Highton & Peabody, 2000	Rissler et al., 2000; Weisrock & Larson, 2006
<i>Plethodon shenandoah</i>	US: Illinois	Y	4	Research (4)	1980, 1982, 1984, 1985	Thurrow, 1999	
<i>Pleurodeles waltl</i>	Azores	?	1			Ferrand de Almeida et al., 2001	
	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	

<i>Proteus anguinus</i>	Spain	N	1					Llorente et al., 1995; Pleguezuelos, 2004
	Belgium	N	1					Parent, 1983
	France	N	1	Research				Arnold & Ovenden, 2002; Pascal et al., 2006
	Italy	Y	1	Intentional	1822			Fitzinger, 1850; Tortonese & Lanza, 1968; Durand, 1997; Sket, 1997; Lapini et al., 1999; Dalla Zuanna et al., 2000; Fracasso et al., 2000
<i>Pseudotriton riberi</i>	Canada: Ontario	N	1	Bait use				FR. Cook, 1984
<i>Salamandra atra</i>	Germany	?	2	Pet trade (2)	1978–1979, 1980s			Eckstein & Meinig, 1989; Münch, 1992
<i>Salamandra salamandra</i>	Azores	?	1					Ferrand de Almeida et al., 2001
(syn: <i>Salamandra maculosa</i>)	Great Britain	N	5	Pet trade	1952			Gadow, 1904; Rigden, 1955; Fitter, 1959; Frazer, 1964; Yálden, 1965; Beebee & Griffiths, 2000
(syn: <i>Salamandra maculosa</i>)	Malta	N	1	Intentional	1910s			Despott, 1913
<i>Speleomantes ambrosii</i>	Italy	Y	2	Research (2)	1983, 1991			Lanza et al., 1995; Lanza, 1997; Cinmaruta et al., 1999; Forti et al., 2005
<i>Speleomantes genei</i> (syn: <i>Hydromantes genei</i>)	Spain	Y	1	Intentional				Lanza, 1997
	Great Britain	N	1	Intentional				J.F.D. Frazer, 1964

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Speleomanes italicus</i> (syn: <i>Hydromantes italicus</i>)	Belgium	N	1			Parent, 1983	
	Italy	Y	1	Research	1983	Lanza et al., 1995; Forti et al., 2005	
<i>Speleomanes strinatii</i> (syn: <i>Speleomanes ambrosii</i>)	France	Y	1	Research	1965	Rivera & Arribas, 1993; Pascal et al., 2006	
<i>Taricha granulosa</i>	US: Montana	?	1			Nussbaum et al., 1983	
<i>Triturus alpestris</i>	France	Y	2		1990	Duguet & Melki, 2003; Denoël, 2005	
	Great Britain	Y	7	Pet trade (3), intentional (2)	1920s, 1940s, 1970, 1974	M. Smith, 1951a; Fitter, 1959; Frazer, 1964; C. Lever, 1977, 1980; A.P. Bell, 1978; Gillett, 1988; Banks, 1989; D. Frazer, 1989; Bell & Bell, 1993, 1995; R. Griffiths, 1996; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002	Beebee, 1995
	Malta	N	1	Intentional	1910s	Despott, 1913	
(syn: <i>Molge alpestris</i>)	Spain	Y	1		1900–1960	de Lope & Cuadrado, 1985; Arano et al., 1991; J. Rivera & Arribas, 1993; Mateo, 1997a; Barbadillo et al., 1999; Pleguezuelos, 2004	Martínez-Solano et al., 2003

<i>Triturus boscai</i>	Spain	N	1	Pet trade	1989	J. Rivera & Arribas, 1993
<i>Triturus carnifex</i>	Austria	?	1			Honegger, 1978
(syn: <i>Triturus cristatus</i> , <i>Triturus cristatus carnifex</i>)	Azores	Y	1	Intentional	<1922	Svanberg, 1975; Malkmus, 1984, 1995, 1998; Machado et al., 1997; Ferrand de Almeida et al., 2001
	Belgium	N	2	Pet trade (2)		Parent, 1983; Jooris, 2000
	France	Y	1	Spread from adjacent introduction	[1987]	Zuiderwijk, 1989; Hafner, 1997; Arnitzen & Thorpe, 1999; Pascal et al., 2006
	Germany	Y	3	Intentional, pet trade (2)	1980, 1983, 1990	Eckstein & Meinig, 1989; Franzen et al., 2002
(syn: <i>Triturus cristatus carnifex</i>)	Great Britain	Y	2	Pet trade (1)		C. Lever, 1977, 1980; Gillett, 1988; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002
	Netherlands	Y	1	Pet trade	1973	Bogaerts et al., 2001; Bogaerts, 2002
(syn: <i>Triturus cristatus carnifex</i>)	Switzerland	Y	1	Research	1940s	Grossenbacher, 1988a, 1988b; Hafner, 1997; Arnitzen & Thorpe, 1999; Arnitzen, 2001; Wittenberg, 2005
	Malta	N	1	Intentional	1910s	Despott, 1913
<i>Triturus cristatus</i> (syn: <i>Molge cristata</i>)	Spain	N	1	Pet trade		J. Rivera & Arribas, 1993
<i>Triturus helveticus</i> (syn: <i>Molge palmata</i>)	Malta	N	1	Intentional	1910s	Despott, 1913
						Vallese et al., 2000

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Spain	N	4	Pet trade		J. Rivera & Arribas, 1993; Barbadillo, 2004; Pleguezuelos, 2004	
<i>Triturus marmoratus</i>	Belgium	N	1	Pet trade		Parent, 1983; Jooris, 2000	
	Spain	Y	1			Pleguezuelos, 2004	
<i>Triturus montandoni</i>	Germany	Y	1			Arnold & Burton, 1978	
<i>Triturus vulgaris</i> (syn: <i>Molge vulgaris</i>)	Malta	N	1	Intentional	1910s	Despott, 1913	
	Switzerland	?	1	Intentional	1940s	Arnitzen & Thorpe, 1999	
	Turkey	Y	1			Kuzmin & Zuidervijk, 1997	
LIZARDS							
<i>Agama agama</i>	Comoros	Y	1		1998	Meirte, 2004	
	Malta	N	1	Cargo stowaway	1979	Schembri & Schembri, 1984; Lanza & Corti, 1993, 1996	
	Spain	N	1	Cargo stowaway		Pleguezuelos, 2004	
	US: Florida	Y	10	Pet trade (8)	1976, mid-1980s (2), 1987, early 1990s, 1999, 2000, 2003 (2), 2006	L.D. Wilson & Porras, 1983; Bartlett & Bartlett, 1999; Enge et al., 2004a; Meshaka et al., 2004a; Krysko et al., 2005; Lechowicz, 2006	Blunden & Krysko, 2007
<i>Agama</i> sp.	US: California	N	1	Pet trade		Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
agamid sp.	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Amblyrhynchus cristatus</i>	Bermuda	N	1	Zoo trade	1933	Wingate, 1965	

<i>Ameiva ameiva</i>	US: Florida	Y	5	Pet trade (3), zoo trade	1953, 1964 (2)	Neill, 1957; Duellman & Schwartz, 1958; W. King & Krakauer, 1966; Bartlett, 1967a; L.D. Wilson & Porras, 1983; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2004a; Krysko et al., 2005.; H.T. Smith et al., 2007b
<i>Ameiva exsul</i>	U.S. Virgin Islands	Y	1			Platenberg & Boulon, 2006
<i>Amphisbaena alba</i>	Great Britain	N	1	Cargo stowaway	1960s	Yalden, 1965
<i>Anguis fragilis</i>	Ireland	Y	2	Intentional (1)	1906	Fitter, 1959; O'Rourke, 1970; McCarthy, 1977; J.P.F. Wilson, 1986; D'Arcy & Hayward, 1992
<i>Anolis aeneus</i>	Malta	N	1	Intentional	1910s	Despott, 1913
	Guyana	Y	1	Nursery trade	Early 1800s	Gorman et al., 1971; Lazell, 1972
	Trinidad	Y	1	Nursery trade	Early 1800s	Gorman & Dessauer, 1966; Gorman et al., 1971; Lazell, 1972; Boos, 1977, 1990; J.C. Murphy, 1997
<i>Anolis baleatus</i>	Surinam	Y	1	Pet trade	1976	Gorman & Atkins, 1968; Gorman & Boos, 1972;
<i>Anolis bimaculatus</i>	St. Maarten	N	1		~1992	Gorman et al., 1978; White & Hailey, 2006
<i>Anolis carolinensis</i>	Anguilla	Y	1	Nursery trade	1990s	Eaton et al., 2001; Hodge et al., 2003

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Bahamas: Grand Bahama	Y	1			Losos et al., 1993	
	Belize: Half Moon Cay	?	1		1966	Henderson & Hoevers, 1975; Stafford & Meyer, 2000	
(syn: <i>Anolis principalis</i>)	Bermuda	N	1		1876	Verrill, 1902; Wingate, 1965	
	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	
	Cayman Islands	?	1			Powell, 2002	
(syn: <i>Anolis porcottus</i>)	CNMI	Y	1		1970s	Vance, 1987; Eldredge, 1988; Wiles et al., 1990; Rodda et al., 1991; Mayer & Lazell, 1992; McCoid, 1999; S.R. Vogt et al., 2001; S.R. Vogt & Williams, 2004	Wiles & Guerrero, 1996
	FSM	Y	1		1968	Mayer & Lazell, 1992	
(syn: <i>Anolis porcottus</i>)	Guam	Y	2	Biocontrol (1)	1953, 1980s	W.C. Brown, 1956; Vance, 1987; Eldredge, 1988; Rodda et al., 1991; Mayer & Lazell, 1992; McCoid, 1993a, 1999	Haddock et al., 1990; Fritts & Rodda, 1998
	Japan: Ogasawara Islands	Y	2	Pet trade	1965	Matsumoto et al., 1980; Hara, 1986; M. Hasegawa et al., 1988; Miyashita, 1991; Suzuki & Nagoshi, 1999; Ota, 2000, 2002a; Goris & Maeda, 2004; Toda & Yoshida, 2005	Ueda & DeForest, 1988; Karube, 2001, 2004a, b, 2005, 2006; Karube & Suda, 2005; Makihara et al., 2004; Takakuwa & Suda, 2004; Yoshimura & Okochi, 2005; Okochi et al., 2006; Toda et al., 2006

Japan: Ryukyu Islands	Y	1	Pet trade	1989	Ota et al., 1995a, 2004a; Ota, 1995, 1999, 2002a; Goris & Maeda, 2004; Toda & Yoshida, 2005
Palau	Y	1		1960s	Eldredge, 1988; Crombie & Pregill, 1999
Spain	N	3	Pet trade (3)	1990s (3)	Mateo, 1997a; Barbadillo et al., 1999; Pleguezuelos, 2004
US: California	N	3	Pet trade (3)	1968	Banta & Morafka, 1966; Bury & Luckenbach, 1976; Jennings, 1987a, 2004
(syn: <i>Anolis porcutus</i>) US: Hawaii	Y	2	Pet trade	1948	Shaw & Breese, 1951; Oliver & Shaw, 1953; Hunsaker & Breese, 1967; Chan et al., 1987; Mayer & Lazell, 1992; McKeown, 1996; J.H. Michael, 1996; Kraus, 2002b; Pansza & Powell, 2005
US: Kansas	Y	3	Pet trade (1)	1938, 1963, 1983	Brumwell, 1942, 1951; Collins, 1993
US: Maryland	N	2	Pet trade (2)		McCauley, 1945
US: Texas	Y	9	Pet trade (2)	1975	Cope, 1900; B.C. Brown, 1950; Mather & Dixon, 1976; Conant, 1977; H.M. Smith & Kohler, 1978; Dixon, 1987, 2000
US: West Virginia	N	1	Pet trade		Green & Pauley, 1987

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Anolis chlorocyanus</i>	Surinam	Y	1	Pet trade	1976	Hoogmoed, 1981	Kolbe et al., 2007a
	US: Florida	Y	4	Pet trade (4)	1978, 1980s	Bartlett, 1988, 1994a; Butterfield et al., 1994a, 1997; McCoid, 1995a; Bartlett & Bartlett, 1999; Meshaka et al., 2004a	
<i>Anolis conspersus</i> <i>Anolis cristatellus</i> (syn: <i>Ctenonotus cristatellus</i>)	US: Florida	N	1	Intentional	1960s	W. King & Krakauer, 1966	
	Costa Rica	Y	1		Early 1970s	Fitch, 1975; Savage, 2002	
	Dominica	Y	1		1997–2002	Powell & Henderson, 2003; Malhotra et al., 2007	
	Dominican Republic	Y	2	Cargo stowaway (1)	1910s	E.E. Williams, 1969, 1977; Schwartz & Henderson, 1991; Kolbe et al., 2007a	Fitch et al., 1989; Zani et al., 1993; Goldberg et al., 1998c
	US: Florida	Y	5	Intentional (3)	1970s (2), 1980s (2), 1998	Schwartz & Thomas, 1975; Brach, 1977; L.D. Wilson & Porras, 1983; Ashton & Ashton, 1985; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Seigel et al., 1999; Meshaka et al., 2004a	Salzburg, 1984; Kolbe et al., 2007a
<i>Anolis cybotes</i>	Surinam	Y	1	Pet trade	1976	Hoogmoed, 1981	

<i>Anolis distichus</i>	US: Florida	Y	4	Intentional (2), pet trade (2)	1960s, 1967, 1986, 1980s	W. King & Krakauer, 1966; Ober, 1973; L.D. Wilson & Porras, 1983; Lazell, 1989a; Butterfield et al., 1994a, 1997; Bartlett & Bartlett, 1999; Townsend et al., 2002; Meshaka et al., 2004a; Krysko et al., 2005	Kolbe et al., 2007a
	Bahamas	Y	1		<1968	Dumdee, 1990; Schwartz & Henderson, 1991; Losos et al., 1993	
<i>Anolis equestris</i>	US: Colorado	N	3	Nursery trade (3)	1989, 1991, 1995	Livo et al., 1998	J.C. Lee, 1980; Miyamoto et al., 1986; Goldberg et al., 1994; Doan, 1996; Meshaka, 1999b, c; Paterson, 1999;
	US: Florida	Y	4	Cargo stowaway, intentional	Early 1960s	H.M. Smith & McCauley, 1948; Duellman & Schwartz, 1958; W. King & Krakauer, 1966; Bartlett, 1967a, 1994a, 1995a; Schwartz, 1968a, 1971; L.D. Wilson & Porras, 1983; Lazell, 1989a; Watkins-Colwell & Watkins-Colwell, 1995a; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Reppas et al., 1999; Meshaka et al., 2000, 2004a; T.S. Campbell & Campbell, 2002	Engel et al., 2004b; Kolbe et al., 2007a
<i>Anolis equestris</i>	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Florida	Y	2	Intentional(1)	1952	Neill, 1957; W. King & Krakauer, 1966; Bartlett, 1967a; L.N. Brown, 1972; Achor & Moler, 1982; L.J. Wilson & Porras, 1983; Noonan, 1995; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2000, 2004a; Krysko et al., 2005; Engle & Coben, 2007; Kolbe et al., 2007a; Krysko & Borgia, 2007a	Brach, 1976; Dalrymple, 1980; Meshaka, 1993, 1999a, b, c; Nicholson & Richards, 1999; Meshaka & Rice, 2001
	US: Hawaii	Y	1	Pet trade	1981	Kishinami & Kishinami, 1996; McKeown, 1996; Lazell & McKeown, 1998	Goldberg et al., 2004b
<i>Anolis extremus</i> (syn: <i>Anolis roquet</i>)	Bermuda	Y	1	Cargo stowaway	Early 1940s	Wingate, 1965; Lazell, 1972; Bacon et al., 2006b	Gorman et al., 1978; Goldberg et al., 1995c; Losos, 1996; Macedonia & Clark, 2003
	St. Lucia	Y	1		1956	Underwood, 1962; Lazell, 1972; Gorman, 1976; Corke, 1992	Gorman et al., 1978; Giannasi et al., 1997
	Trinidad	Y	2	Research	1965	Boos, 1967, 1977, 1978; J.C. Murphy, 1997	
	US: Florida	?	1	Pet trade	1990s	Bartlett & Bartlett, 1999; Meshaka et al., 2004a	
	Venezuela	Y	1			Lazell, 1972	
<i>Anolis ferreus</i>	US: Florida	Y	1	Pet trade	1990	Bartlett, 1994a; Bartlett & Bartlett, 1999; Meshaka et al., 2004a	

<i>Anolis garmani</i>	Cayman Islands	N	1				Schwartz & Henderson, 1991; Seidel & Franz, 1994
	US: Florida	Y	3	Intentional (1), pet trade (1)	Early 1970s, 1985, 1986		L.D. Wilson & Porras, 1983; Ashton & Ashton, 1985; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2004a
<i>Anolis grahami</i> (syn: <i>Anolis iodurus</i>)	Bermuda	Y	1	Biocontrol	1905		Dunn & Conant, 1937; Wingate, 1965; Bacon et al., 2006b
<i>Anolis leachii</i> (syn: <i>Anolis bimaculatus</i>)	Bermuda	Y	1		1940		Wingate, 1965; Lazell, 1972; Bacon et al., 2006b
<i>Anolis lineatus</i>	U.S. Virgin Islands Klein Curaçao	Y Y	1 1	Intentional	2005		Perry, 2005 van Buurt, 2006
<i>Anolis lucius</i>	Surinam Cuba: Archipelago de los Canarreos	Y Y	1 1	Pet trade	1974		Hoogmoed, 1981 Schwartz & Henderson, 1991
<i>Anolis marmoratus</i>	French Guiana	Y	1	Cargo stowaway	<1950		Hoogmoed & Lescure, 1975; Mittermeier & Plotkin, 1980; Hoogmoed, 1981
<i>Anolis maynardi</i>	Cayman Islands	Y	1	Cargo stowaway	Mid-1970s		Franz et al., 1987; Seidel & Franz, 1994
<i>Anolis porcatius</i>	Dominican Republic	Y	1	Cargo stowaway	1955		Swartz & Thomas, 1975; Haneline, 1977; E.E. Williams, 1977; Vance, 1987; Powell, 1990a, 1992; Powell et al., 1990; Powell & Parmelee, 1991; Gifford et al., 2002
							Gorman et al., 1978; Griffith & Wingate, 1994; Goldberg et al., 1995c; Losos, 1996; Davenport et al., 2001; Macedonia & Clark, 2003
							R.W. Williams, 1959; Gorman et al., 1978; Goldberg et al., 1995c; Losos, 1996; Macedonia & Clark, 2003
							Lescure & Fretey, 1977
							Goldberg & Bursley, 1996
							Powell, 1990b; Parmelee et al., 1992; Kolbe et al., 2007a

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Florida	Y	3	Cargo stowaway (1)	1936, 1987	Allen & Slatten, 1945; Vance, 1987; Meshaka et al., 1997a, 2004a; Bartlett & Bartlett, 1999	Meshaka, 1999b, c; Townsend, 2003; Kolbe et al., 2007a
<i>Anolis pulchellus</i>	Puerto Rico: Isla Palominos	N	1	Research	1964	Levins & Heatwole, 1973	
<i>Anolis richardii</i>	Surinam Tobago	N Y	1 1	Pet trade	1973	Hoogmoed, 1981 Gorman et al., 1978; J.C. Murphy, 1997	
<i>Anolis sagrei</i>	Canary Islands Cayman Islands: Grand Cayman	N Y	1 1	Pet trade Nursery trade		Pleguezuelos, 2004 Minton & Minton, 1984; Franz et al., 1987; Seidel & Franz, 1994	J.C. Lee, 1992; Losos et al., 1993; Goldberg et al., 1995d; Gerber & Echternacht, 2000; Kolbe et al., 2004, 2007b
	Grenada	Y	1	Cargo stowaway	1990s	B.T. Greene et al., 2002	J.M. Germano et al., 2003; Kolbe et al., 2004
	Jamaica	Y	1			Underwood & Williams, 1959; E.E. Williams, 1969; Landwer et al., 1995; Kolbe et al., 2004	Schoener & Schoener, 1971; Bundy et al., 1987; Landwer & Ferguson, 2002
	Mexico	Y	1			Calderon et al., 2003; Zamora-Abrego et al., 2006	
	St. Vincent	Y	1			Henderson & Powell, 2005	
	Taiwan	Y	1	Nursery trade	1990s	Norval et al., 2002; Lue et al., 2003	Kolbe et al., 2004; Norval et al., 2006
(<i>syn: Norops sagrei</i>)	US: Alabama US: Arkansas	Y ?	1 1	Nursery trade	2005 2002	Steffen & Birkhead, 2007 C.T. McAllister et al., 2003	

- (syn: *Anolis stegeneri*,
Anolis stejnegeri)
- US: Florida
- Y 8
- Cargo stowaway 1887, 1940s,
(5), inten- 1941, 1945,
tional (1), pet 1946, 1960,
trade (1) 1964
- Garman, 1887; Barbour,
1931a; Carr, 1940;
Allen & Slatten, 1945;
J.A. Oliver, 1950;
L.N. Bell, 1953;
Duellman & Schwartz,
1958; W. King, 1960;
Ruilbal, 1964; W. King
& Krakauer, 1966;
Corwin et al., 1977;
Layne et al., 1977;
P. Meylan, 1977a;
Myers, 1978a, 1981;
Funk & Moll, 1979;
Wygodá & Bain, 1980;
Godley et al., 1981;
L.D. Wilson & Porras,
1983; Winegarner
et al., 1984; Steiner
& McLamb, 1985;
P.A. Cochran, 1990;
Means, 1990a, 1996a;
Franz et al., 1992; D.
Stevenson & Crowe,
1992b; T.S. Campbell
& Hammonree, 1995a;
T. Campbell, 1996a, b,
2003a; Butterfield et al.,
1997; Christman et al.,
2000; Meshaka et al.,
2000, 2004a; Townsend
& Lindsay, 2001;
Dodd & Griffey, 2002;
Townsend et al., 2002;
D.C. Bishop, 2005; D.R.
Jackson, 2007
- Neill, 1951a, b; D.S. Lee, 1969; J.C.
Lee, 1980, 1985, 1987, 1992;
Lieb et al., 1983; Hammer,
1984; Okafor et al., 1984; Price
& Underwood, 1984; Salzburg,
1984; Mushinsky, 1985;
Tokarz, 1985, 1986, 1987a, b,
1988, 1989, 1992, 1995, 1998,
1999, 2002, 2006, 2007; Sellers
& Graham, 1987; Tokarz
& Beck, 1987; Dalrymple,
1988; P.A. Cochran, 1989;
J.C. Lee et al., 1989; Tokarz &
Slowinski, 1990; P.R. Brown
& Echemacht, 1991; Gerber,
1991; Minesky & Echemacht,
1991; Tokarz & Kirkpatrick,
1991a, b; Meshaka, 1993;
Dalrymple, 1994; B.W.
Kaiser & Mushinsky, 1994;
T. Campbell & Gerber, 1996;
Doan, 1996; Tokarz et al.,
1998, 2002, 2003, 2005;
T. Campbell, 1999a, 2000;
Echemacht, 1999; Meshaka,
1999c; Vincent, 1999; Gerber
& Echemacht, 2000; McMaam,
2000; Nicholson et al., 2000;
Franz, 2001; Paterson, 2002;
T.S. Campbell & Echemacht,
2003; McMaam & Paterson,
2003a, b; Burger et al., 2004;
Enge et al., 2004b; Kolbe et al.,
2004, 2007b; Paterson &
McMaam, 2004; K.R. Campbell
& Campbell, 2005; McKie
et al., 2005; Batareau &
Leblanc, 2006; Perkins
et al., 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Georgia	Y	11	Nursery trade (1), vehicle (9)	1987, 1991, 1992, 1994 (5), 1995, 1990s, 2002	T.S. Campbell & Hammontree, 1995b; Echternacht et al., 1995; Campbell, 1996a; Parmley, 2002; Skelton & Parmley, 2005	
	US: Hawaii	Y	2	[Nursery trade, pet trade]	1980	Kishinami & Kishinami, 1996; McKeown, 1996; Kraus, 2002b, 2003a, 2006; Powell & Pausza, 2005	Goldberg & Bursley, 2000a; Goldberg et al., 2002a, b; Kolbe et al., 2004; Muenssch et al., 2006
	US: Louisiana	Y	8	Nursery trade (6), pet trade (1)	1975, 1980s (2), 1993, 2000, 2001, 2006 (2)	R.A. Thomas et al., 1990; Platt & Fontenot, 1994; Boundy, 2004; Wiley et al., 2007	Kolbe et al., 2007b
	US: Ohio	N	1	Nursery trade		Meshaka et al., 2004a	
	US: South Carolina	?	3			Turnbough, 2006	
	US: South Dakota	N	1	Nursery trade		Meshaka et al., 2004a	
	US: Tennessee	N	1	Nursery trade		Meshaka et al., 2004a	
	US: Texas	Y	7	Nursery trade (6)	1984 (3), 1985, 2003, early 2000s	Dixon 1987, 2000; K. King et al., 1987; Krusing et al., 1995a; McCoïd, 2006	Kolbe et al., 2007b
	US: Virginia	N	2	Nursery trade	1978	Mitchell, 1982, 1994	
	Isla Palominos	N	1	Research	1965	Levins & Heatwole, 1973	
	Trinidad	Y	1	Nursery trade	Early 1800s	Gorman & Dessauer, 1966; Gorman et al., 1971; Lazell, 1972; Boos, 1977; J.C. Murphy, 1997	Gorman & Atkins, 1968; Gorman & Boos, 1972; Gorman et al., 1978
	<i>Anolis stratulus</i>						
	<i>Anolis trinitatis</i>						

<i>Anolis wattsi</i>	Anguilla St. Lucia	N Y	3 1	Research (3)	1979, 1980, 1981 1956	Roughgarden et al., 1984 Lazell, 1972; Gorman, 1976; Corke, 1992
<i>Anolis</i> sp.	Trinidad	Y	1	Nursery trade	1977–1991	White & Hailey, 2006 Boos, 1977
	Trinidad	N	2			Minton, 1972
<i>Aspidoscelis motaguae</i> (syn: <i>Cnemidophorus</i> <i>motaguae</i>)	US: Indiana	N	2	Nursery trade	1986	Cardoza et al., 1993
	US: Massachusetts	N	1			Bartlett, 1995b; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2004a
	US: Florida	Y	2	Pet trade (2)		
	US: New Mexico	Y	1			Leuck et al., 1981; J.M. Walker et al., 1992; Taylor, 2002
<i>Aspidoscelis neomexi- cana</i> (syn: <i>Cnemidophorus</i> <i>neomexicanus</i>)	US: Oregon	Y	1			Storm & Leonard, 1995
<i>Aspidoscelis velox</i>	US: Florida	N	1	Pet trade	1960s	W. King & Krakauer, 1966
<i>Basiliscus basiliscus</i>	US: Florida	N	1			Butterfield et al., 1997;
<i>Basiliscus plumifrons</i>	US: Florida	N	3	Pet trade (3)	1990s (3)	Bartlett & Bartlett, 1999; Meshaka et al., 2004a; Krysko et al., 2006
<i>Basiliscus vittatus</i>	US: Florida	Y	3	Pet trade (3)	1970s (2)	L.D. Wilson & Porras, 1983; Dalrymple, 1994; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2004a; Krysko et al., 2005, 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Brachylophus fasciatus</i>	Vanuatu	Y	1	Pet trade	1970s	J.R.H. Gibbons, 1981; C. Morrison, 2003	
<i>Bradypodion pumilum</i> (syn: <i>Chamaeleon pumilus</i>)	Greece	N	1			Schreiber, 1912	
<i>Calotes mystaceus</i> (syn: <i>Calotes versicolor</i>)	Namibia US: Florida	Y Y	2 2	Pet trade (2)	1970s (2) Early 1980s	M. Griffin, 2000 Butterfield et al., 1997; Bartlett & Bartlett, 1999; Engel & Krysko, 2004; Meshaka et al., 2004a	
<i>Calotes versicolor</i>	Andaman Islands	Y	1			Das, 1999	
(syn: <i>Agama versicolor</i>)	Chagos Archipelago Mauritius	Y Y	1 1	Cargo stowaway Biocontrol	2001 1900	Kraus, 2003b Koenig, 1932; J. Vinson & Vinson, 1969; Blanc, 1972; Cheke, 1987; Tonge, 1990; Staub, 1993	
	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
	Oman	Y	1			Arnold, 1986; Seuffer et al., 1999; van der Kooij, 2000, 2001b	
(syn: <i>Agama versicolor</i>)	Réunion	Y	1	Nursery trade	1865	Koenig, 1932; J. Vinson & Vinson, 1969; Blanc, 1972; Bour & Moutou, 1982; Cheke, 1987	
	Seychelles Singapore	Y Y	1 1		1982	Matyot, 2004 Lim & Chou, 1990; Lim & Lim, 1992; Chou, 1994; Diong et al., 1999; Diong & Ho, 2001	

	US: Florida	Y	1	Pet trade	1978	Engé & Krysko, 2004; Meshaka, 2006	
<i>Carlita ailanpalatai</i> (syn: <i>Carlita fusca</i>)	CNMI	Y	1		1950s	Dryden & Taylor, 1969; Wiles et al., 1989; Rodda et al., 1991; Wiles & Guerrero, 1996; McCoid, 1999; S.R. Vogt et al., 2001; S.R. Vogt & Williams, 2004	Rodda, 1992a; Fritts & Rodda, 1998
	FSM	Y	1			Zag, 2004	
(syn: <i>Carlita fusca</i> , <i>Carlita fuscum</i> , <i>Carlita</i> sp.)	Guam	Y	1		1960s	Rodda et al., 1991; McCoid, Ota et al., 1988; Haddock et al., 1990; Rodda, 1992a; Fritts & Rodda, 1998; Perry et al., 1998b; S.R. Vogt & Williams, 2004	
<i>Carlita schmelzii</i>	Australia	N	1		1998	Limpus et al., 1999	
<i>Carlita tutela</i> (syn: <i>Carlita fusca</i>)	Palau	Y	1		1980s	Crombie & Peggill, 1999	
<i>Carlita</i> sp.	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Chalcidoides chalcidoides</i>	Belgium	N	1			Parent, 1983	
<i>Chalcidoides ocellatus</i> (syn: <i>Gongylus ocellatus</i>)	France	N	1	Intentional	1900	Stépi, 1913; Monticelli, 1914	
(syn: <i>Gongylus</i> <i>ocellatus</i>)	Great Britain Italy	N Y	1 1	Cargo stowaway Cargo stowaway	1738-1770	Fitter, 1959 Monticelli, 1902, 1914; Lanza, 1973; Lanza & Corti, 1993, 1996; Caputo et al., 1997; B. Schneider, 1997	
<i>Chalcidoides sextineatus</i>	Madeira	Y	1			Pasteur, 1981; Bringsøe, 1993	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Chalcides viridanus</i>	Canary Islands Madeira	Y Y	1 1			Pleguezuelos, 2004 Pasteur, 1981; Bringsøe, 1993; Mateo, 1997a	
<i>Chamaeleo africanus</i> (syn: <i>Chamaeleon vulgaris</i> , <i>Chamaeleo chamaeleon</i>)	Greece	Y	1			Schreibler, 1912; Böhme, 1989; Böhme et al., 1998; Kosuch et al., 1999	Dimaki et al., 2000a, b, 2001; Lutzmann, 2001
<i>Chamaeleo calyptrotus</i>	US: Florida	Y	4	Pet trade (4)	2000, 2002	Krysko et al., 2004; Meshaka, 2006	
<i>Chamaeleo chamaeleon</i>	US: Hawaii Canary Islands	Y N	1 1	Pet trade Pet trade	1990s	Kraus & Duvall, 2004 Mertens & Wermuth, 1960; Honegger, 1978; Bischoff, 1985; Rodríguez Luengo, 2001; Pleguezuelos, 2004	
(syn: <i>Chamaeleon vulgaris</i>)	France Greece: Crete	N Y	1 1			Schreibler, 1912 ŠiŠpánek, 1934; Vétstein, 1953; Klaver, 1981; Dimitropoulos, 1987; Blasco, 1997	Snowden, 1987
(syn: <i>Chamaeleon vulgaris</i>)	Italy	?	1	Pet trade	Early 1980s	Basso & Calasso, 1991; Lanza & Corti, 1993, 1996; Fattizzo, 1996; Bagnoli & Carpaneto, 2000; Fattizzo & Marzano, 2002; Razzetti & Sindaco, 2006	
	Italy: Sicily	?	18	Cargo stowaway (12), pet trade (5)	<1830, 1960s (17)	Schreibler, 1912; Bruno, 1970; Klaver, 1981; Lanza & Corti, 1993, 1996; Razzetti & Sindaco, 2006	

(syn: <i>Chamaeleon vulgari</i>)	Malta	Y	1	Intentional	Š1880	Gulia, 1890, 1909, 1914; Despoit, 1915; Lanza, 1973; Savona-Ventura, 1974, 1985; Schembri, 1983; Schembri & Schembri, 1984; Lanza & Corti, 1996	Savona-Ventura, 1975; Jacobsen, 1993; Luiselli & Rugiero, 1996; Bruekers, 2003a
	Portugal	Y	1	Intentional	Š1920	Themido, 1945; Crespo, 1973; Malkmus, 1995; Blasco, 1997a, b; Blasco & Gonzalez, 1997; Cuadrado & Rodriguez de los Santos, 1997; Barbadillo et al., 1999; Ferrand de Almeida et al., 2001; Paulo et al., 2002	Bogaerts, 1989; Hofman et al., 1991; Peek & Bogaerts, 1995
	Spain	Y	5	Pet trade (4)		Gadow, 1909; de Oliveira, 1931; Alvarez López, 1934; Blasco, 1978, 1997a, b; Blasco et al., 1979; Klaver, 1981; Blasco and Romero, 1985; Blasco & Gonzalez, 1997; Cuadrado & Rodriguez de los Santos, 1997; Mateo, 1997a; Barbadillo et al., 1999; Goncé & Ruiz, 1999; Rivilla et al., 2000; Mellado et al., 2001; Hernández et al., 2002; Paulo et al., 2002; Salvador & Pleguezuelos, 2004	Ramón y Cajal, 1900; Blasco, 1979; Blasco et al., 1985a, b, 2001; Romero, 1985; Fernández, 1988, 1989, 1994; Hofman et al., 1991; Fernández & Cuadrado, 1992; Cuadrado, 1996, 1997, 1998a-d, 1999, 2000a,b, 2001, 2002; Cuadrado & Loman, 1997, 1999; Cuadrado & Rodríguez de los Santos, 1997; Pleguezuelos et al., 1999; Blázquez et al., 2000; Hódar et al., 2000; Cuadrado et al., 2001, 2002; Díaz-Paniagua et al., 2002a, b; Poveda et al., 2002; Padilla et al., 2004; Díaz-Paniagua, 2007

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Chamaeleo gracilis</i>	US: Florida	?	1			Engeman et al., 2005a	
<i>Chamaeleo jacksonii</i>	US: California	Y	1	Pet trade	1981	McKeown, 1997	
	US: Hawaii	Y	1	Pet trade	1972	McKeown, 1991, 1996; Kraus, 2006	Goldberg et al., 2004c
<i>Chlamydosaurus kingii</i>	Indonesia: Biak	Y	1	Intentional	1993	Günther & Kapisa, 2003	
<i>Chondrodactylus bibronii</i> (syn: <i>Pachydactylus bibronii</i>)	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
(syn: <i>Pachydactylus bibronii</i>)	South Africa	Y	4	Intentional, pet trade (3)	1960s (3)	Rose, 1950; Siegfried, 1962; Brooke et al., 1986	
(syn: <i>Pachydactylus bibronii</i>)	US: Florida	Y	1	Intentional	1970s	Bartlett & Bartlett, 1999; Meshaka et al., 2004a	
<i>Christinus marmoratus</i>	New Zealand	N	2	Cargo stowaway (2)		Gill et al., 2001	
<i>Cnemidophorus lemniscatus</i>	Aruba	Y	1	Cargo stowaway	1950	van Buurt, 2005	Schall, 1973
(syn: <i>Cnemidophorus picturatus</i>)	Belize	Y	1		1990s	J.C. Lee, 2000	
	US: Florida	Y	1	Pet trade	1964	W. King & Krakauer, 1966; L.D. Wilson & Porras, 1983; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2004a	Punzo, 2001a
<i>Conolophus subcristatus</i>	Ecuador: Galapagos Islands	Y	2	Conservation (2)	1932, 1933	Banning, 1933; S. Campbell, 1978; Reynolds, 1981; Woram, 1992; Cayot et al., 1994	

<i>Cordylus cordylus</i>	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966
<i>Cordylus giganteus</i>	US: California	N	1	Pet trade	1970s	Jennings, 1987a, 2004
<i>Cordylus jonesii</i> (syn: <i>Cordylus tropidosternum jonesi</i> , <i>Zonurus jonesi</i> , <i>Zonurus jonesii</i>)	South Africa	N	3	Cargo stowaway (2), nursery trade	1988	Hewitt & Power, 1913; Siegfried, 1962; Brooke et al., 1986; Branch & Braack, 1990; Bourquin, 2004
<i>Cordylus</i> sp. (syn: <i>Zonurus</i> sp.)	US: California	N	1	Pet trade		Bury & Luckenbach, 1976; Jennings, 1987a, 2004
<i>Crotaphytus collaris</i>	US: Colorado	?	1	Intentional	1991	Livo et al., 1998
<i>Cryptoblepharus carnabyi</i>	Australia	?	1	Cargo stowaway		R. Bennett, 1997
<i>Cryptoblepharus plagi- ocephalus</i>	Australia	Y	3	Cargo stowaway (3)	1980s (3)	Bush, 1987; Low, 2003
<i>Cryptoblepharus poecilopleurus</i> (syn: <i>Ablepharus boutonii</i> , <i>Ablepharus poecilopleurus</i> , <i>Cryptoblepharus boutonii</i>)	New Zealand	N	1	Cargo stowaway		Gill et al., 2001
<i>Cryptoblepharus virgatus</i>	US: Hawaii	Y	1	Cargo stowaway	\$400	Stejneger, 1899; McGregor, 1904; Tinker, 1938; Fisher, 1948; Oliver & Shaw, 1953; Hunsaker & Brese, 1967; Lazell, 1986, 1989b; McKeown, 1996
	Australia	Y	1	Cargo stowaway	1960s	Heatwole, 1978; Limpus et al., 1999
	New Zealand	N	2	Cargo stowaway (2)		Gill et al., 2001
<i>Ctenosaura conspicuosa</i> (syn: <i>Ctenosaura hemilopha</i>)	Mexico: Sea of Cortez islands	Y	2	Food (2)		Lowe & Norris, 1955; Grismer, 1994b, 2002a, b; Nabhan, 2002

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Ctenosaura hemilopha</i>	US: California	N	1	Research		Stebbins, 1972; Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
<i>Ctenosaura pectinata</i> (syn: <i>Ctenosaura similis</i>)	US: Florida	Y	1	Pet trade	1960s	Eggert, 1978; L.D. Wilson & Porras, 1983; Dalrymple, 1994; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2000, 2004a; Townsend et al., 2003a, b	
	US: Texas	Y	2	Pet trade		Conant, 1977; Dixon, 1987, 2000	
<i>Ctenosaura similis</i> (syn: <i>Ctenosaura pectinata</i>)	Canary Islands US: Florida	N Y	1 5	Pet trade Intentional (1), pet trade (3), zoo trade (1)	Late 1970s, 1979, 1994, 1995, 1996	Pleguezuelos, 2004 Butterfield et al., 1997; Bartlett & Bartlett, 1999; McCoid, 2002a; Erratum, 2003; Krysko et al., 2003a; Townsend et al., 2003a, b; Meshaka et al., 2004a; Engel et al., 2006; Olson et al., 2007	Hinggen, 1995; Engeman et al., 2007
<i>Ctenopus</i> sp.	New Zealand	N	2	Cargo stowaway (2)		Gill et al., 2001	
<i>Cyclura cornuta</i>	Surinam US: Florida	? N	1 2	Pet trade Zoo trade	1976	Hoogmoed, 1981 W. King & Krakauer, 1966; Bartlett, 1967a; Bartlett & Bartlett, 1995a	

<i>Cyclura nubila</i> (syn: <i>Cyclura macleanyi</i>)	Cayman Islands	Y	1	Food			C. Grant, 1940; Schwartz & Carey, 1977; Seidel & Franz, 1994
<i>Cyrtopodion scabrum</i>	Puerto Rico	Y	1	Zoo trade	Mid-1960s		Schwartz & Carey, 1977; Rivero, 1978; Christian, 1986; R. Thomas & Joglar, 1996
(syn: <i>Cyrtodactylus scaber</i>)	Egypt	Y	1	Cargo stowaway			Baha el Din, 1994, 2000, 2006
<i>Cyrtodactylus</i> (syn: <i>Cyrtodactylus scaber</i>)	Israel	Y	1	Cargo stowaway	1980s		Hoofien, 1995; Crochet, 1997; Wernet, 1998; Bouskila & Amitai, 2001
<i>Cyrtodactylus</i> (syn: <i>Cyrtodactylus scaber</i>)	US: Texas	Y	1	Cargo stowaway	Early 1980s		Seleer & Bloom, 1984; Bloom et al., 1986; Dixon, 1987, 2000
<i>Darevskia armeniaca</i> (syn: <i>Lacerta armeniaca</i>)	Ukraine	Y	1	Research	1963		Darevsky, 1997, 2006
<i>Darevskia mixta</i>	Ukraine	N	1	Research	1968		Darevsky, 2006
<i>Darevskia valentini</i> (syn: <i>Podarcis muralis</i>)	US: Ohio	N	1	Cargo stowaway	1986		Conant & Collins, 1998; Bischoff & Deichsel, 2002; Deichsel & Bischoff, 2002; Deichsel, 2004
<i>Diplodactylus ciliaris</i>	New Zealand	N	1	Cargo stowaway			Robb, 1986
<i>Ebenavia thunguis</i>	Mauritius	Y	1				Cheke, 1987; Tonge, 1990
<i>Egernia cunninghami</i>	New Zealand	N	1				West, 1979
<i>Egernia depressa</i>	Australia	N	1	Cargo stowaway			Bush, 1987

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Egernia formosa</i>	Singapore	N	1	Cargo stowaway	1925	Chasen, 1925	
<i>Egernia stokesii</i>	Australia	N	1	Cargo stowaway		Bush, 1987	
<i>Elgaria multicarinata</i>	Australia	N	1	Vehicle	1997	Duffield & Bull, 2002	
	US: California	Y	1	Cargo stowaway		Mahoney et al., 2003	
	US: Massachusetts	N	1		1938	Cardoza et al., 1993	
<i>Emoia cyanura</i>	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
	US: Hawaii	Y	1	Cargo stowaway		Lazell, 1986; McKeown, 1996	
<i>Emoia impar</i>	Peru	?	1		1883	Dunn, 1936; Ineich & Zug, 1991	
(syn: <i>Emoia cyanura</i>)	US: Hawaii	Y	1	Cargo stowaway	~400	Stejneger, 1899; McGregor, 1904; Tinker, 1938; Oliver & Shaw, 1953; Hunsaker & Breese, 1967; McKeown, 1996	Snyder, 1917; La Rivers, 1948; Baldwin et al., 1952
<i>Eulamprus quoyii</i> (syn: <i>Sphenomorphus quoyii</i>)	New Zealand	N	1	Cargo stowaway		West, 1979; Gill et al., 2001	
<i>Eulamprus</i> sp. (syn: <i>Sphenomorphus tenuis</i>)	Australia	Y	1	Cargo stowaway	1960s	Heatwole, 1978; Limpus et al., 1999	
<i>Eumeces obsoletus</i>	US: California	N	1	Pet trade		Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
<i>Furcifer pardalis</i> (syn: <i>Chamaeleo pardalis</i>)	Mauritius	N	1			Cheke, 1987	
<i>Furcifer verrucosus</i>	Mauritius	N	1			Cheke, 1987	

<i>Gallotia atlantica</i>	Canary Islands	Y	1	Early 1900s	Barquín & Martín, 1982; Báez, 1987; Mateo, 1997a; Mateo & López-Jurado, 1997a; Pleguezuelos, 2004	González et al., 1996
<i>Gallotia caesaris</i>	Canary Islands	Y	1		Pleguezuelos, 2004	
<i>Gallotia galloti</i>	Canary Islands	Y	1	1990s	Cargo stowaway	Rodríguez-Domínguez and Ruiz-Caballero, 1998; Barbadillo et al., 1999; Pleguezuelos, 2004
	Madeira	N	2	<1839, \$1990		Richter, 1986a; Bringsøe, 1993; Malkmus, 1995; Jesus et al., 2002
<i>Gallotia stehlini</i>	Canary Islands	Y	2	Early 1900s	Cargo stowaway	Naranjo et al., 1991; Mateo, 1997a; Mateo & López-Jurado, 1997b; Pleguezuelos, 2004
<i>Gehyra dubia</i>	Australia	?	1			Messenger, 2005
<i>Gehyra mutilata</i>	Christmas Island	Y	1	>1945		Cogger et al., 1983a; Cogger, 1992
	Clipperton Island	Y	1	1893–1958		Lorvelec & Pascal, 2006
	Cocos-Keeling Island	Y	1	>1835		Wood Jones, 1909; Gibson-Hill, 1950; Cogger et al., 1983a; Cogger, 1992
	Cook Islands	Y	1	>1800	Cargo stowaway	Crombie & Steadman, 1987
	Fiji	Y	1			C. Morrison, 2003
	French Guiana	Y	1	Early 1990s		Ineich & de Massary, 1997
	India	?	1			Das, 1998
						Goldberg & Burse, 2002b Zug, 1991; Goldberg & Burse, 2002b

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Madagascar	Y	1			Boulenger, 1909; Glaw & Vences, 1992	
	Mauritius	Y	1	Cargo stowaway	Before 1800	Cheke, 1987; Tonge, 1990	
	Mexico	Y	1	Cargo stowaway	16th/17th century	Boulenger, 1909; E.H. Taylor, 1922, 1940; H.M. Smith & Taylor, 1950; H.M. Smith & Grant, 1958; Hardy & McDiarmid, 1969; Alvarez del Toro, 1982; Reynoso, 1990a; Flores-Villela, 1993; Grismer, 1994a, 2002a; Ponce-Campos & Huerta-Ortega, 2001; Quijada-Mascareñas & Canseco-Marquez, 2007a	
	New Zealand	N	5	Cargo stowaway (5)	1949	McCann, 1955; Robb, 1973, 1986; West, 1979; Gill et al., 2001	
	Réunion	Y	1	Cargo stowaway		Bour & Moutou, 1982; Cheke, 1987	
	Rodrigues	Y	1	Cargo stowaway		J. Vinson, 1964; Cheke, 1987	
	Seychelles	Y	1		1860s	Boulenger, 1909; Cheke, 1984; Matyot, 2001	Ineich & Ineich, 1993
	Seychelles: Aldabra Atoll	Y	1		1977	Cheke, 1984	

	US: California	N	2	Zoo trade	1944	Shaw, 1946a; Jennings, 1987a, 2004
	US: Florida	?	2	Pet trade	1996, 1997	Meshaka et al., 2004a
	US: Hawaii	Y	1	Cargo stowaway	\$400	Girard, 1858; Stejneger, 1899; McGregor, 1904; Fowler, 1914; Tinker, 1938; Fisher, 1948; Oliver & Shaw, 1953; Hunsaker & Brese, 1967; Lazell, 1989b; McKeown, 1996
	(syn: <i>Dactyloperus insulensis</i> , <i>Peropus mutilatus</i>)					McMorris, 1970; Quay, 1974; Decker et al., 2003; Goldberg et al., 2004a
	Vanuatu	N	1		1924	Medway & Marshall, 1975; Cranbrook, 1985
	New Zealand	N	11	Cargo stowaway (11)		Hutton, 1904; McCann, 1955; Sharell, 1966; Robb, 1973, 1986; West, 1979; Gill et al., 2001
	Australia	N	4	Cargo stowaway (4)		Bush, 1987
	Australia	N	1	Cargo stowaway	1997	Limpus et al., 1999
	New Zealand	N	5	Cargo stowaway (5)		Gill et al., 2001
	Australia	N	1			Boulenger, 1885; R.A. Cook, 1990
	Guam	N	1	Cargo stowaway	1983	McCoid, 1993a
	Japan: Ryukyu Islands	?	1			Ota, 1995, 1999
	Madagascar	?	1			W.C. Brown & Alcalá, 1978
	Martinique	Y	1	Intentional	1973	Henderson et al., 1993

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	New Zealand	N	2	Cargo stowaway (2)		Gill et al., 2001	
	Samoa	?	1			W.C. Brown & Alcalá, 1978	
	US; Florida	Y	17	Biocontrol (1), intentional (2), pet trade (4)	Early 1960s, 1963, 1964, 1990, 1990s	W. King & Krakauer, 1966; Bartlett, 1967a; Layne et al., 1977; L.D. Wilson & Porras, 1983; Means, 1996b; Duquesnel, 1998; Bartlett & Bartlett, 1999; Butterfield & Hauge, 2000; Love, 2000; Meshaka et al., 2004a; Krysko et al., 2005; Krysko & Daniels, 2005	Meshaka et al., 1997b; Love, 2000
<i>Gekko hokouensis</i>	US; Hawaii Japan; Izu Islands	Y Y	1 1	Pet trade Nursery trade	Late 1960s >1960	McKeown, 1996 Ota et al., 1995b; M. Hasegawa, 1999; Toda & Yoshida, 2005	
<i>Gekko japonicus</i>	Japan; mainland Japan; mainland	Y Y	3 2			Toda & Yoshida, 2005 Toda & Yoshida, 2005	
<i>Gekko monarchus</i>	New Zealand	N	2	Cargo stowaway (2)		Gill et al., 2001	
<i>Gekko ulikovskii</i>	South Africa	N	1	Cargo stowaway	2002	Bauer & Branch, 2004	
<i>Gekko</i> sp.	US; Florida New Zealand	? N	1 1	Pet trade Cargo stowaway	2003	Engel et al., 2004a Gill et al., 2001	
gekkonid sp.	New Zealand	N	2	Cargo stowaway (2)		Gill et al., 2001	

<i>Gonatodes albogularis</i>	Aruba	Y	1		Wagenaar Hummelinck, 1940; van Buurt, 2005
	Belize	Y	1	1996	J.C. Lee, 2000; Stafford & Meyer, 2000
	Cayman Islands	N	1		E.E. Williams, 1964; Seidel & Franz, 1994
	Colombia	Y	1		Rueda-Almonacid, 1999
	Curaçao	Y	1		Wagenaar Hummelinck, 1940; van Buurt, 2005
	Mexico	Y	1		H.M. Smith & Taylor, 1950; Flores-Villela, 1993
(syn: <i>Gonatodes fuscus</i>)	US: Florida	Y	3	Cargo stowaway, pet trade	Carr, 1939, 1940; Duellman & Schwartz, 1958; W. King & Krakauer, 1966; Bartlett, 1967a; L.D. Wilson & Porras, 1983; Lawson et al., 1991; Bartlett, 1994b; Bartlett & Bartlett, 1995b, 1999; Butterfield et al., 1997; Meshaka et al., 2004a; Krysko & Daniels, 2005
<i>Gonatodes antillensis</i>	Aruba	Y	1		van Buurt, 2005
<i>Gonatodes caudiscutatus</i>	Ecuador: Galapagos Islands	Y	1	Cargo stowaway	J.W. Wright, 1983a; M.H. Jackson, 1985; Hoogmoed, 1989; Olmedo & Cayot, 1994
(syn: <i>Gonatodes collaris</i> , <i>Gonatodes collaris</i>)				Late 1800s	
<i>Gonatodes vittatus</i>	Aruba	Y	1		van Buurt, 2005
	Dominica	N	1	[Cargo stowaway, nursery trade]	Malhotra et al., 2007

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Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Gymnophthalmus underwoodi</i>	Antigua	Y	1			Dalry, 2007	
<i>Heloderma horridum</i>	Barbuda US: California	Y N	1 1	Pet trade		Censky & Lindsay, 1997 Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
<i>Heloderma suspectum</i>	US: California	N	1	Pet trade		Bury & Luckenbach, 1976	
<i>Hemidactylus brookii</i>	US: Indiana China	N Y	1 1			Minton, 1972 Romer, 1978b; Karsen et al., 1998	
	Comoros	Y	1			Vences et al., 2004b	
	Honduras	Y	1			Köhler, 2003	
	Hong Kong	Y	2	Cargo stowaway	1970s	Romer, 1978a; Karsen et al., 1998	
(syn: <i>Hemidactylus mabouia</i> , <i>Hemidactylus mercatorius</i>)	Mauritius New Zealand Panama	Y N Y	1 1 1	Cargo stowaway		Tonge, 1990; C. Lever, 2003; Vences et al., 2004b Gill et al., 2001 Ibáñez et al., 1992; Auth, 1994; Köhler, 2003	
(syn: <i>Hemidactylus mabouia</i> , <i>Hemidactylus mercatorius</i>)	Réunion	Y	1			Bour & Moutou, 1982; Cheke, 1987; C. Lever, 2003; Vences et al., 2004b	
	Rodrigues	Y	1			Vences et al., 2004b	
	Seychelles	Y	1			Cheke, 1984	
	US: Florida	N	3	Intentional (3)	1960s, 1963, 1964	W. King & Krakauer, 1966	

<i>Hemidactylus flaviviridis</i>	Egypt	Y	1	Cargo stowaway	Parker, 1932; Loveridge, 1947; Saleh, 1997; Ibrahim, 2000; Bahael Din, 2006	Saoud et al., 1995; Ibrahim & Ghobashy, 2004
	Eritrea	Y	1		Parker, 1932; Loveridge, 1947	
	Somalia	Y	1		Parker, 1932; Loveridge, 1947	
	Sudan	Y	1		Parker, 1932; Loveridge, 1947; Rössler & Wraniak, 2005	
	Yemen: Socotra	Y	1			
<i>Hemidactylus frenatus</i>	American Samoa	Y	1	1960s	Amerson et al., 1982; Case et al., 1992; Petren et al., 1993	Schwaneer, 1980; Burseay & Goldberg, 1996a
	Australia	Y	1	Cargo stowaway	Hunsaker, 1967; Cogger et al., 1978, 1983b; Heatwole, 1978; Fyfe, 1981; R.A. Cook, 1990; Storr et al., 1990; Covacevich & Couper, 1991; Cogger, 1992; Elhmann, 1992; Bauer & Henle, 1994; S.K. Wilson & Czechura, 1995; Anthony, 1996; Limpus et al., 1999; Low, 1999; Lloyd, 2000; Bedford & Padovan, 2001; Maryan, 2001; Swan et al., 2004; D.R. Michael, 2005; S. Wilson, 2005	M. King, 1978; Husband, 1980; Börner & Schüttler, 1982; P. Wright, 1982; Greer, 1989; Zahari et al., 1990; Domrow, 1991; Newbery et al., 2005
	Australia: Ashmore Reef	Y	1		Horner, 2005	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Australia: Norfolk Island	?	2	Cargo stowaway (2)	2000 (2)	Covacevich et al., 2001	
	Belize	Y	1			J.C. Lee, 2000; Stafford & Meyer, 2000; Rainwater & Platt, 2001	
	Christmas Island	Y	1		1900	Gibson-Hill, 1950; Hunsaker, 1967; Cogger et al., 1983a; Cogger, 1992	
	Cocos-Keeling Island	Y	1		1930s	Gibson-Hill, 1950; Cogger et al., 1983a; Cogger, 1992	
	Comoros	Y	1	Cargo stowaway		Meirte, 2004; Vences et al., 2004b	
	Cook Islands	Y	1		>1940	Fisher, 1997	Goldberg & Burse, 2002b
	Costa Rica	Y	1	Cargo stowaway	1990s	Kronauer, 1999; Savage, 2002; Köhler, 2003	Barquero & Hijje, 2005; Frenkel, 2006
	El Salvador	Y	1			Greenbaum, 2002; Köhler, 2003; Köhler et al., 2006; Herrera et al., 2005, 2007	
	Fiji	Y	1		1960	J.R.H. Gibbons, 1985; Case & Bolger, 1991; Zug, 1991; Petren et al., 1993; Case et al., 1992, 1994; Shea, 1995; C. Morrison, 2003	Bolger & Case, 1992; Moritz et al., 1993; Case et al., 1994; Hanley et al., 1995; Burse & Goldberg, 1996a; Goldberg & Burse, 2002b
	French Polynesia	Y	1		1988	Case & Bolger, 1991; Case et al., 1992, 1994; Petren et al., 1993; Ineich et al., 2007	Moritz et al., 1993; Case et al., 1994; Hanley et al., 1995; Burse & Goldberg, 1996a; Goldberg & Burse, 2002b

FSM	Y	1	>1940	Petren et al., 1993; Case et al., 1994; Fisher, 1997; Buden, 2000a; Buden et al., 2001
Guatemala	Y	1		Auth, 1994; Köhler, 2003
Honduras	Y	1		Franklin, 2000; Köhler, 2001, 2003
Hong Kong	?	1	1989	Karsen et al., 1998
Japan: mainland	N	1	2003	Takahashi, 2005
Japan: Ogasawara Islands	Y	1		Hara, 1986; Ota, 2000; Toda Ota, 1994 & Yoshida, 2005
Japan: Ryukyu Islands	Y	2	<1854	Hunsaker, 1967; Toyama, 1984a; Ota, 1989, 2000; Kohno & Ota, 1991; Toyama & Ota, 1991; Nohima et al., 1998; Kuze & Ota, 2001; Toda et al., 2003; Ota et al., 2004a; Tanaka, 2004; Toda & Yoshida, 2005
Johnston Atoll	Y	1		Bauer & Henle, 1994
Kiribati	Y	1		Bauer & Henle, 1994
Loyalty Islands	Y	1	1940s	Sadlier & Bauer, 1997; Bauer & Sadlier, 2000
Madagascar	Y	1		Angel, 1942; Vences et al., 2004b
Marquesas	Y	1		Haitlinger, 1988; Upton et al., 1990
Marshall Islands	Y	1	>1940	Bauer & Henle, 1994
				Petren et al., 1993; Case et al., 1994; Fisher, 1997
				Hanley et al., 1995; Burse & Goldberg, 1996a; Goldberg & Burse, 2002b

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Mauritius	Y	1			Tonge, 1990; C. Lever, 2003; Vences et al., 2004b	Arnold, 2000; Cole, 2005; Cole et al., 2005; Leinwand et al., 2005
	Mexico	Y	1		1920s	E.H. Taylor, 1940; Burt & Myers, 1942; H.M. Smith, 1942; Edgren, 1950; H.M. Smith & Taylor, 1950; Chrapliwy, 1956; C. Grant, 1957; Pianka & Smith, 1959; Hunsaker, 1967; Hardy & McDiarmid, 1969; Limer & Dundee, 1969; Marcellini, 1971a; Webb, 1972; Stebbins, 1985; Franco, 1987; Reynoso, 1990b; Castro-Franco & Bustos Zagal, 1994; Grismet, 1994a, 2002a; Schmidt Ballardo et al., 1996; J.C. Lee, 1996, 2000; Powell et al., 1998; Casas-A. et al., 1998; Galina-Tessaró et al., 1999; McPeak, 2000; Cedeño-Vázquez et al., 2003; Köhler, 2003; B.R. Norman, 2003; Calderón-Mandujano & Mora-Tembre, 2004; Paredes-León & Reynoso, 2005, 2006	Marcellini, 1971b, 1974, 1976, 1977, 1978; Ramirez-Bautista et al., 2006

Nauru	Y	1					Bauer & Henle, 1994
New Caledonia	Y	1	1942				Bauer & Vindum, 1990; Gargominy et al., 1996; Bauer, 1999; Bauer & Sadlier, 2000
New Zealand	N	41		Cargo stowaway (41)			Gill et al., 2001; Anonymous, 2005
Nicaragua	Y	1	1988–1998				Vences et al., 1998; Köhler, 1999, 2003
Palau	Y	1	1955	Cargo stowaway			Crombie & Pregill, 1999 Case et al., 1994; Hanley et al., 1995; Bursley & Goldberg, 1996a; Goldberg & Bursley, 2002b
Palmyra	Y	1					Bauer & Henle, 1994
Panama	Y	1					Rand & Myers, 1990; Auth, 1994; Jaramillo et al., 1994; Köhler, 2003
Papua New Guinea	Y	1					Bauer & Henle, 1994 Bustard, 1970; Domrow, 1983; Pernetta & Black, 1983
Réunion	Y	1					Maillard, 1862; Bour & Moutou, 1982; Cheke, 1987; Vences et al., 2004b
Rodrigues	Y	1					J. Vinson, 1964; Cheke, 1987; Vences et al., 2004b
Samoa	Y	1	1960s				Case et al., 1992, 1994; Gill, 1993 Moritz et al., 1993; Case et al., 1994; Hanley et al., 1995; Bursley & Goldberg, 1996a; Goldberg & Bursley, 2002b

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Seychelles	Y	1			Matyot, 2003	
	Solomon Islands	Y	1		>1940	M. McCoy, 1980; Fisher, 1997	Moritz et al., 1993; Case et al., 1994; Hanley et al., 1995; Bursley & Goldberg, 1996a; Goldberg & Bursley, 2002b
	Somalia	?	1			J. Vinson & Vinson, 1969	
	South Africa	?	1			Savage, 2002	
	St. Helena	Y	1	Cargo stowaway	<1875	Melliss, 1875; Mertens, 1934; Loveridge, 1959; J. Vinson & Vinson, 1969; Basilewsky, 1970; Ashmole & Ashmole, 2000	
	Taiwan	Y	1			Hunsaker, 1967; Lue et al., 1987, 1992; Ota, 1989, 2000; Lue et al., 2003	Cheng & Lin, 1977, 1978; Jaing & Lin, 1980; Lin & Cheng, 1984; Cheng, 1987a, 1988
	Tonga	Y	1		>1940	Fisher, 1997	
	US: Florida	Y	3	Pet trade (3)	1993	Meshaka et al., 1994a, 2004a; Bartlett & Bartlett, 1999; Townsend & Krysko, 2003; Krysko et al., 2005; Krysko & Daniels, 2005; Krysko & Sheehy, 2005	Krysko et al., 2003c

US: Hawaii	Y	1	Cargo stowaway	1940s	Hunsaker, 1967; Hunsaker & Breese, 1967; McCoy & Busack, 1970; McMorris, 1970; Lazell, 1989b; McKeown, 1996	R.E. Jones, 1979; Schwaner, 1980; Frankenberg & Werner, 1981; R.E. Jones & Summers, 1984; Tenorio, 1985; Huey et al., 1989; Werner, 1990a, b; Watermolen, 1992, 2005; Moritz et al., 1993; Petren et al., 1993; Case et al., 1994; Upton et al., 1994; S.G. Brown et al., 1995, 1998, 2002; Hanley et al., 1995, 1998; Bursley & Goldberg, 1996a; Murphy-Walker & Haley, 1996; Petren & Case, 1996, 1998; Goldberg & Bursley, 2000b; Dame & Petren, 2006
US: Texas	Y	2	Zoo trade (1)	1970s, 1988	C.T. McAllister et al., 1990; Saenz & Klawinski, 1996	
Vanuatu	Y	1		1970s-1980s	Case & Bolger, 1991; Case et al., 1992	Moritz et al., 1993; Case et al., 1994; Hanley et al., 1995; Bursley & Goldberg, 1996a; Goldberg & Bursley, 2002b
Venezuela	Y	1			Rivas Fuenmayor et al., 2005	
Wake Island	Y	1			Bauer & Henle, 1994	
Bahamas	Y	2	Nursery trade	1992	Buckner & Franz, 1994a; Meshaka, 1995a, 1996a; D.S. Lee, 2004, 2005	
Cook Islands	Y	1	Cargo stowaway	>1800	Crombie & Steadman, 1987	Moritz et al., 1993; Bursley & Goldberg, 2000
Costa Rica	Y	1		1992	Savage, 2002; Köhler, 2003	
New Zealand	N	3	Cargo stowaway (3)		McCann, 1955; Robb, 1973, 1986; West, 1979; Gill et al., 2001	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Samoa	Y	1	Cargo stowaway	>1943	Crombie & Steadman, 1987; Gill, 1993	
	St. Helena	?	1			Savage, 2002	
	US: California	N	1	Zoo trade	1944	Shaw, 1946	
	US: Florida	Y	3	Cargo stowaway (1), intentional (2)	1950s (1), early 1960s (2)	W. King & Krakauer, 1966; Kluge & Eckardt, 1969; McCoy, 1972; S. Myers, 1978b, 1979; Mitchell & Hadley, 1980; Steiner & McLamb, 1982; R.E. Smith, 1983; L.D. Wilson & Porras, 1983; Lazell, 1989a; D. Stevenson & Crowe, 1992c; Crawford & Sonima, 1993b; Meshaka et al., 1994b, 2000, 2004a; Franz, 1995; Meshaka, 1996a; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Reppas, 1999; Christman et al., 2000; Lindsay & Townsend, 2001; Dodd & Griffey, 2002; McCoid, 2002b; Townsend et al., 2002; Erratum, 2003; Klowden, 2003; Townsend & Krysko, 2003; Johnston & Johnston, 2004; Townsend & Lindsay, 2004; Krysko et al., 2005; Krysko & Daniels, 2005; Himes & Enge, 2007	Voss, 1975; Dunson, 1982; Frankenberg, 1982a, 1984; Steiner, 1983; Moritz et al., 1993; Meshaka, 1994a, 2000, 2001; Punzo, 2001b; Eifler et al., 2004; Enge et al., 2004b; Meshaka et al., 2005a, 2006b; Dame & Petren, 2006

<i>(syn: Doryura vulpecula)</i>	US: Hawaii	Y	1	Cargo stowaway	\$400	Girard, 1858; Stejneger, 1899; McGregor, 1904; H.W. Fowler, 1914; Tinker, 1938; Fisher, 1948; Oliver & Shaw, 1953; Hunsaker & Breese, 1967; Kluge & Eckardt, 1969; Lazell, 1989b; McKeown, 1996	Snyder, 1917; La Rivers, 1948; Baldwin et al., 1952; McMorris, 1970; Eckardt & Whimster, 1971; Tenorio, 1985; Moritz et al., 1993
	US: Texas	Y	1	Nursery trade	1996	Franklin, 1996	
<i>Hemidactylus leschen-aultii</i>	Mauritius	N	1		Early 1800s	Cheke, 1987	
	Réunion	N	1		Early 1800s	Cheke, 1987	
<i>Hemidactylus mabouia</i>	Argentina	Y	1		Early 2000s	Federico & Cacivio, 2000	
	Aruba	Y	1		Early 2000s	van Buurt, 2005, 2006	
	Bahamas	Y	1		1991	Franz et al., 1993; Buckner & Franz, 1994b; D.S. Lee, 2004, 2005; Krysko & Borgia, 2005; Krysko & Thomas, 2007	
	Bonaire	Y	1		1990s	van Buurt, 2005, 2006	
	Cape Verde Islands	Y	1		2001	Jesus et al., 2001	
	Cayman Islands	Y	1			Echternacht & Burton, 2002	
	Costa Rica	Y	1			Abarca & Monge, 2007	
	Cuba	Y	1			Barbour, 1937; Buiide, 1967; Kluge, 1969; Schwartz & Henderson, 1991; Powell et al., 1998; Estrada & Ruibal, 1999	Coy Otero & Baruš, 1979; Martínez Rivera et al., 2003
	Curaçao	Y	1		Late 1980s	van Buurt, 2005, 2006	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Dominican Republic	Y	1			Schwartz & Henderson, 1991; Powell et al., 1998	
	Equatorial Guinea	Y	1			Jesus et al., 2003, 2005	
	Haiti	Y	1			Schwartz & Henderson, 1991; Powell et al., 1998	
	Honduras	Y	1		1998	McCramie & Wilson, 2000; Köhler, 2003	
	Jamaica	Y	2			Fläschendräger, 1999	
	Klein Bonaire	Y	1			van Buurt, 2006	
	Madeira	Y	1		1990s	Jesus et al., 2002	
	Mexico	Y	1			H.M. Smith and Taylor, 1950; Flores-Villela, 1993; Powell et al., 1998	C.T. McAllister & Upton, 1989
	Panama	Y	1			Auth, 1994; Köhler, 2003	
	Puerto Rico	Y	1			Powell et al., 1998; Mayer, 1999; R. Thomas, 1999	Martínez Rivera et al., 2003
	São Tomé & Príncipe	Y	1			Jesus et al., 2005	
	South Africa	Y	6	Cargo stowaway (3), intentional (2)	1962, 1976, 1980, 1986 (2)	Brooke et al., 1986; Branch, 1987; Bourquin, 1987, 2004	
	Surinam	Y	1	Cargo stowaway	Mid 1960s	Hoogmoed, 1981	
	Turks and Turks & Caicos	Y	1			Minton & Minton, 1975	

Uruguay	Y	1		Carreira et al., 2005	
US: Florida	Y	2	[Cargo stowaway, nursery trade]	Lawson et al., 1991; Butterfield et al., 1993, 2000; R. Günther et al., 1993; Meshaka et al., 1994b, 1994c, 2004a; Watkins-Colwell & Watkins-Colwell, 1995b; Meshaka & Moody, 1996; Criscione et al., 1998; Bartlett & Bartlett, 1999; Bihovde & Owen, 2002; Klowden, 2002; Townsend et al., 2002; Van Dyke, 2004; Krysko et al., 2005; Krysko & Sheehy, 2005; Krysko & Daniels, 2005; Krysko & Camposano, 2007; Krysko & Somma, 2007	Bock, 1996; Meshaka & Moody, 1996; Meshaka, 2000, 2001; Punzo, 2001b; Krysko et al., 2003c; Regalado, 2003; Eifler et al., 2004; Enge et al., 2004b; Meshaka et al., 2005a, 2006b
Venezuela	Y	1	Cargo stowaway	Mijares-Urrutia & Arends, 2000; Rivas Fuenmayor, 2001; Rivas et al, 2001; Rivas Fuenmayor et al., 2005	
<i>Hemidactylus mercatorius</i>	Y	1		Vences et al., 2004b	
<i>Hemidactylus platyurus</i> (syn: <i>Cosymbotus platyurus</i>)	N	2	Cargo stowaway (2)	Gill et al., 2001	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
(syn: <i>Cosymbotus platyurus</i>)	US: Florida	Y	4	Pet trade (4)	1981, 1990s (3)	Meshaka & Lewis, 1994; Butterfield, et al., 1997; Bartlett & Bartlett, 1999; Hauge & Butterfield, 2000a; Meshaka et al., 2004a	
<i>Hemidactylus turcicus</i>	Argentina	Y	1			J.D. Williams, 1988; Cei, 1993	
	Balearic Islands	Y	1			Alcover & Mayol, 1981; J. Rivera & Ambas, 1993; Esteban et al., 1994; Palerm, 1997; Mayol, 2003; Pleguezuelos, 2004	Rodríguez Ruiz, 1974; Salvador, 1978, 1993; Roca, 1993
	Canary Islands	Y	1	Cargo stowaway		Loweridge, 1947; Báez, 1979, 1987; Salvador, 1981; Mellado, 1982; Bischoff, 1985; López-Jurado, 1991; Mateo, 1997a; Rodríguez Luengo, 2001; Pleguezuelos, 2004	Trujillo et al., 1995
	Chile	?	1			McCoy, 1970	
	Cuba	Y	1			Leavitt, 1933; Barbour, 1937; Buide, 1967; McCoy, 1970; Estrada & Ruibal, 1999; Rodríguez Schettino, 2000	Baruš & Coy-Otero, 1974; Coy Otero & Baruš, 1979
	Great Britain	N	1	Cargo stowaway	1964	Yalden, 1965	
	India	Y	1			Flower, 1933	
	Italy	Y	2	Cargo stowaway (1)	2000	Lapini et al., 1996; Fracasso & Bonato, 2000	

Mexico	Y	1	Cargo stowaway	Barbour & Cole, 1906; Barbour, 1937; H.M. Smith & Taylor, 1950; Conant, 1955; McCoy, 1970; Easterla, 1978; Salvador, 1981; Alvarez del Toro, 1982; J.C. Lee, 1996, 2000; Martinez-Isac & Valdés-Villavicencio, 2000; Lemos-Espinal et al., 2001; Köhler, 2003
New Zealand	N	2	Cargo stowaway (2)	Gill et al., 2001
Panama	Y	1		McCoy, 1970; Schwartz & Henderson, 1991; Auth, 1994; Köhler, 2003
Puerto Rico	Y	1		Conant & Collins, 1991
US: Alabama	Y	5		Mount, 1975; Marion & Bosworth, 1982; Dundee, 1984; Nelson & Carey, 1993; Dowling, 1996
US: Arizona	Y	3	1965, 1970	Robinson & Romack, 1973; Rosen & Schwalbe, 2002; Goodward et al., 2005
US: Arkansas	Y	1	1972	Paulissen & Buchanan, 1990; White & Tumison, 1999; Manning & Briggler, 2003; Sheehy, 2004; Fowler & Robison, 2007
				Paulissen & Buchanan, 1991
				Goldberg et al., 2000
				Trout & Schwaner, 1994

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: California	Y	1	Cargo stowaway	1980s	Porter, 1988; De Lisle, 1989; Saethre & Medica, 1993; Jennings, 2004; Beaman et al., 2005	
	US: Colorado	N	1	Cargo stowaway	1995	Livo et al., 1998	
	US: Florida	Y	1		1910	Fowler, 1915; Stejneger, 1922; Barbour, 1936, 1937; Carr, 1940; Mittleman, 1950; Duellman & Schwartz, 1958; W. King, 1960; L.N. Brown & Hickman, 1970; McCoy, 1970, 1971; Layne et al., 1977; P. Meylan, 1977b; S. Myers, 1978c, d; L.D. Wilson & Porras, 1983; Ashton & Ashton, 1985; Means, 1990b, 1996c, 1999; Nelson & Carey, 1993; Wise, 1993; Jensen, 1995; Criscione et al., 1998; Bartlett & Bartlett, 1999; Collins & Irwin, 2001; Townsend & Reppas, 2001; S.A. Johnson et al., 2002; Townsend et al., 2002; Townsend & Krysko, 2003; Meshaka et al., 2004a; Krysko et al., 2005; Krysko & Daniels, 2005	Neill, 1951a, b; W. King, 1959; Frankenberg, 1982b, 1984; Sakaluk & Belwood, 1984; Frankenberg & Marcellini, 1990; Meshaka et al., 1994a, b; Meshaka, 1995b; Punzo, 2001b, c; Eifler et al., 2004; Gomez-Zlatar & Moulton, 2005

US: Georgia	Y	1	1981	Bechtel, 1983; Mills, 1990; Frick, 1997; M.P. Greene et al., 2007
US: Illinois	Y	1	2000s	McDowell et al., 2006
US: Kansas	Y	1	2005	Hare, 2006
US: Louisiana	Y	1	1945	Etheridge, 1952; Viosca, 1957; Conzelmann & Thomas, 1971; Dundee & Rossman, 1989; S.L. Jensen & George, 1993; Boundy, 1994; Vidrine & Hatler, 1995; Burke, 1996; Watkins-Colwell et al., 1996; A.A. Williams, 1997; Ray & Cochran, 1997; Boundy, 2004; L.M. Hardy et al., 2005; Meshaka et al., 2006c; Sylvester et al., 2007
US: Maryland	Y	1	1974	Norden & Norden, 1989; Bauer, 2000; Harris, 2004
US: Mississippi	Y	2	1976	Keiser, 1984; Nelson & Carey, 1993
US: Missouri	Y	1	2003	Bufalino, 2004
US: Nevada	Y	2		Saethre & Medica, 1993; Reed et al., 2006a

(continued)

Rose & Barbour, 1968; C.T. McAllister et al., 1988; J.H. Slade et al., 1995; Criscione & Font, 2001; Paulissen et al., 2004

Trout & Schwaner, 1994

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: New Mexico	Y	1		1991	Painter et al., 1992; Degenhardt et al., 1996; Sias & Humphrey, 2002; Murray & Painter, 2003; Byers et al., 2007	
	US: Oklahoma	Y	12	Biocontrol (5), cargo stowaway (1)	1962, 1963, 1964, 1965, 1960s, 1985, 1980s, 1997	Henniger & Black, 1987; J. Murphy, 1987; Sievert & Sievert, 1993; Lardie, 2001; Locey & Stone, 2006	Locey & Stone, 2007
	US: South Carolina	Y	1		1990s	Eason & McMillan, 2000	
	US: Texas	Y	1	Cargo stowaway	1945	Conant, 1955; Dixon, 1958, 1987, 2000; E.D. Morrison, 1961; Treadwell, 1962; W.K. Davis, 1967, 1972, 1974; McCoy, 1970; Keown, 1972; Raun & Gehlbach, 1972; Merkord, 1975; Easterla, 1978; Price, 1980; Selcer, 1986; Calaway et al., 1988; Cheatham, 1988; Schaefer & Kasper, 1989; Pajjak & McCord, 1993; Vaughan, 1993; Krusing et al., 1995b; Husak, 1996; Proudfoot & McCoid, 1996; J.R. Smith et al., 1996; Franklin, 1997;	Trauth, 1985; Selcer, 1986, 1987, 1990, 1992; C.T. McAllister et al., 1988, 1990, 1991, 1993; Pence & Selcer, 1988; J. Riley et al., 1988; Upton et al., 1988; Huey et al., 1989; Frankenberg & Marcellini, 1990; Longoria, 1993; Klawinski et al., 1994; Saenz, 1996; Saenz & Conner, 1996; Vaughan et al., 1996; Limer, 1997; McCoid & Hensley, 1997; Angilletta et al., 1999; D.T. Roberts et al., 1999; Carman et al., 2000; Hitchcock & McBrayer, 2006; McCallum & McCallum, 2006a, b

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Mauritius	Y	1			Bour & Moutou, 1982; Cheke, 1987; Tonge, 1990	
	New Zealand	N	2	Cargo stowaway (2)		Gill et al., 2001	
	Réunion	Y	1			Bour & Moutou, 1982; Cheke, 1987	
	Rodrigues	Y	1			Bour & Moutou, 1982; Cheke, 1987	
	Taiwan	Y	1			Ota, 1989, 2000; C. Lever, 2003; Lue et al., 2003	Ota & Ross, 1990; Lin, 1994
	US: California	N	1	Zoo trade	1944	Shaw, 1946	
(syn: <i>Hemiphyllodactylus leucostictus</i> , <i>H. albobstictus</i>)	US: Hawaii	Y	1	Cargo stowaway	§400	Stejneger, 1899; Tinker, 1938; Fisher, 1948; Oliver & Shaw, 1953; Hunsaker & Breese, 1967; Lazell, 1989b; McKeown, 1996	Snyder, 1917
<i>Holbrookia maculata</i>	US: Colorado	N	1	Pet trade	1907	Livo et al., 1998	
	US: Missouri	N	1		1967	Nickerson & Krager, 1972	
<i>Iguana delicatissima</i>	Puerto Rico	?	1			C. Lever, 2003	
<i>Iguana iguana</i>	Anguilla	Y	1	Pet trade		Hodge et al., 2003; Powell, 2004	
	Antigua	Y	1			Powell, 2004; Powell et al., 2005	

Barbuda	Y	1				Powell, 2004; Powell et al., 2005
British Virgin Islands	Y	1				MacLean, 1982; R. Thomas & Jøglar, 1996; Lazell, 2005; Perry & Gerbet, 2006
Canary Islands	Y	1	Pet trade	1990s		Rodriguez Luengo, 2001; Pleguezuelos, 2004
Cayman Islands	Y	1		1980s–1990s		Seidel & Franz, 1994; C. Lever, 2003
Guadeloupe	Y	1				Breuil, 2000b, 2002
Guadeloupe: Marie-Galante	Y	1		1995		Breuil, 2002; Lorvelec et al., 2007
Guam	N	1	Pet trade	1983–1984		McCoid, 1993a
Japan: Ogasawara Islands	N	1	Pet trade			Shimizu, 1995
Martinique	Y	1	Zoo trade	1960s		Breuil, 2000a, 2002; Lorvelec et al., 2007
Puerto Rico	Y	2	Pet trade (2)	1974		Rivero, 1978; McCoid, 1995a; R. Thomas & Jøglar, 1996; Dyer et al., 1999; R. Thomas, 1999
Spain	N	6				Pleguezuelos, 2004
St. Maarten	Y	1	Pet trade	1995		Breuil, 2002; Powell, 2004; Powell et al., 2005; Lorvelec et al., 2007

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	U.S. Virgin Islands	Y	1			MacLean, 1982; R. Thomas & Jøglar, 1996	
	US: California	N	4	Pet trade (4)		Banta & Morafka, 1966; Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
	US: Florida	Y	7	Pet trade, zoo trade	1964	W. King & Krakauer, 1966; Bartlett, 1967a; L.D. Wilson & Porras, 1983; Butterfield et al., 1997; Duquesnel, 1996, 1998; Bartlett & Bartlett, 1999; Meshaka et al., 2000, 2004a; Townsend et al., 2002, 2003b; Krysko et al., 2005, 2007a	Engeman et al., 2005c; McKie et al., 2005; Meshaka et al., 2004b, 2007; Townsend et al., 2005; H.T. Smith et al., 2006a, 2007a, b
	US: Hawaii	Y	1	Pet trade	1950s	McKeown, 1996; Kraus, 2006	
	US: Indiana	N	1			Minton, 1972	
	US: Massachusetts	N	2	Pet trade	1992 (1)	Cardoza et al., 1993	
	US: Texas	?	2		1990s	Meshaka et al., 2004b	
	Japan: mainland	Y	1		Early 1990s	Ota et al., 2006	
<i>Japalura pobygonata</i>	Malta	N	1	Intentional	1910s	Despott, 1913	
<i>Lacerta agilis</i>							

<i>Lacerta bilineata</i> (syn: <i>Lacerta viridis</i>)	Great Britain	Y	9	Intentional (7)	1872, 1899, 1905–1910, 1931, 1937, 1958, 1960s, 1962, 1990s	Swanton, 1928; R.H.R. Taylor, 1948, 1963; J.F.D. Frazer, 1949, 1964; M. Smith, 1951a; Fitter, 1959; Yalden, 1965; Spellerberg, 1975; C. Lever, 1977, 1980; Walters, 1981; D. Frazer, 1989; Amann et al., 1997; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002; Gleed-Owen, 2004; Deichsel et al., 2007
(syn: <i>Lacerta viridis</i>)	Ireland	N	1	Intentional	1958	Cabot, 1965; O'Rourke, 1970; McCarthy, 1977; C. Lever, 1980; D'Arcy & Hayward, 1992
(syn: <i>Lacerta viridis</i>)	US: Kansas	Y	1	Pet trade	1950s	Collins, 1993, 1997; Gubanyi, 1996, 2000; Gubanyi & Gubanyi, 1997; Deichsel & Miller, 2000; Kalyabina-Hauf & Deichsel, 2002
(syn: <i>Lacerta viridis</i>)	US: New Jersey	N	1	Cargo stowaway	1940s	Conant, 1945
<i>Lacerta trilineata</i> (syn: <i>Lacerta srrigata trilineata</i>)	Austria	N	2	Intentional (2)	Early 1950s (1)	Sochurek, 1958, 1978; Eisel, 1961; Cabela, 1990; Geiger & Waitzmann, 1996
<i>Lacerta</i> sp. (syn: <i>Lacerta viridis</i>)	Belgium	N	1			Parent, 1983

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
(syn: <i>Lacerta viridis</i>)	Malta	N	1	Intentional	1964	Lanfranco, 1964	
<i>Lamprolepis smaragdina</i>	CNMI	Y	1		1960s–1970s	Eldredge, 1988; Wiles et al., 1989; Rodda et al., 1991; Wiles & Guerrero, 1996; McCoid, 1999; S.R. Vogt & Williams, 2004	Wiles & Guerrero, 1996; Perry & Buden, 1999
	Guam	N	1	Intentional	Late 1960s	Eldredge, 1988; Rodda et al., 1991; McCoid, 1993a, 1999	
<i>Lampropholis delicata</i>	Australia: Lord Howe Island	Y	1	Cargo stowaway	1972–1997	C. Lever, 2003; Low, 2003; Hutchinson et al., 2005	
(syn: <i>Leiolopisma delicata</i> , <i>Leiolopisma delicata</i>)	New Zealand	Y	3	Cargo stowaway (3)	1960s	Sharell, 1966; Robb, 1973, 1974, 1986; Bull & Whitaker, 1975; West, 1979; Lark, 1984; Gill, 1986; Gill & Whitaker, 1996; C. Lever, 2003; Gill et al., 2001	
(syn: <i>Leiolopisma hawaiiensis</i> , <i>Leiolopisma metallica</i> , <i>Lygosoma hawaiiensis</i> , <i>Lygosoma metallicum</i>)	US: Hawaii	Y	1	Cargo stowaway	1900–1909	Loveridge, 1939; Brongersma, 1942; Fisher, 1948; Oliver & Shaw, 1953; Hunsaker & Brese, 1967; McCoy & Busack, 1970; Quay, 1973; K. Baker, 1976; J.K. Baker, 1980; Lazell, 1986; McKeown, 1996; Kraus, 2002b	K. Baker, 1976; J.K. Baker, 1980; Goldberg et al., 2004a

<i>Lampropholis guichenoti</i>	New Zealand	N	1	Cargo stowaway	Gill et al., 2001
<i>Lampropholis</i> sp.	New Zealand	N	2	Cargo stowaway	Gill et al., 2001
<i>Laudakia stellio</i>	Egypt	Y	1		Flower, 1933; Daan, 1967; Baha el Din, 2006
	Greece	Y	1		Daan, 1967
(syn: <i>Agama stellio</i>)	Greece: Corfu	Y	1	Cargo stowaway	Mertens, 1961, 1968a; Daan, 1967; Arnold & Ovenden, 2002; Tóth et al., 2002
	Malta	Y	1		Arnold & Ovenden, 2002
	Morocco	N	1		Daan, 1967
	US: Florida	N	2	Pet trade (2)	Engel et al., 2004a; Meshaka et al., 2004a
<i>Leiocephalus carinatus</i>	US: Florida	Y	5	Intentional, zoo trade (3)	Barbour, 1936; Duellman & Schwartz, 1958; W. King, 1960; W. King & Krakauer, 1966; Weigl et al., 1969; Truitt & Ober, 1971; L.D. Wilson & Porras, 1983; Ashton & Ashton, 1985; Layne, 1987; Bartlett, 1994; Dalrymple, 1994; Duquesnel, 1996, 1998; Hauge & Butterfield, 2000b; Krysko & King, 2002b; McCoid, 2002c; H.T. Smith & Engeman, 2002, 2004a; H.T. Smith & Engeman, 2003, 2004b, 2007; Dean et al., 2005a, b; Meshaka et al., 2006c; H.T. Smith et al., 2006b, c, d

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Leiocephalus personatus</i>	US: Florida	?	2	Pet trade (2)	1970s, 1990	T.S. Campbell & Klowden, 2003; Dean et al., 2004a, b; Meshaka et al., 2004a, 2005b, 2006d; M.M. Smith et al., 2004; Krysko et al., 2005, 2007c; Krysko & Borgia, 2007b	
<i>Leiocephalus schreibersi</i>	US: Florida	Y	1	Pet trade	1978	Bartlett, 1994a; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2004a L.D. Wilson & Porras, 1983; Bartlett, 1994; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Townsend et al., 2002; Meshaka et al., 2004a; Krysko et al., 2005	
<i>Leiolepis belliana</i>	US: Florida	Y	1	Pet trade	Early 1990s	Krysko & Enge, 2005; Meshaka, 2006	
<i>Lepidodactylus aureo-lineatus</i>	Indonesia: Sulawesi	?	1	Cargo stowaway	1930s	Zug, 2006	
<i>Lepidodactylus etaensis</i>	New Zealand	N	3	Cargo stowaway (3)		Gill et al., 2001	

<i>Lepidodactylus lugubris</i>	Australia	Y	2	Cargo stowaway (2)	1950s, 1995	Cogger et al., 1983b; R. Russell, 1986; Covacevich & Couper, 1991; Cogger, 1992; Ehmann, 1992; Limpus et al., 1999; Low, 1999; C. Lever, 2003; S. Wilson, 2005	Mau, 1978; Moritz et al., 1993; O'Brien, 1994; Turner & Green, 1996; Messenger, 2005
Brazil	Y	1			Girard, 1858; Mechler, 1968; Auth, 1994; Manthey & Grossmann, 1997; Rueda- Almonacid, 1999		
Chile	Y	1			Röll, 2002		
Christmas Island	Y	1			C. Lever, 2003		
Colombia	Y	1			Kluge, 1966; Ayala, 1986; Ineich, 1999; Rueda- Almonacid, 1999; Moreno-Arias et al., 2006		
Costa Rica	Y	1			Auth, 1994; Savage, 2002		
Ecuador	Y	1			Mechler, 1968; Schauenberg, 1968; Hoogmoed, 1989; Rueda-Almonacid, 1999; Torres-Carvajal, 2001		
Ecuador: Galapagos Islands	Y	1			Hoogmoed, 1989; Olmedo & Cayot, 1994; Sengoku, 1998		
Japan: Ogasawara Islands	Y	1			Uchiyama et al., 2002; Toda & Yoshida, 2005; Yamashiro & Ota, 2005		

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Japan; Ryukyu Islands	Y	3		1971	Shibata et al., 1972; Hayashi et al., 1983; Shibata, 1983; Toyama & Miyagi, 1984; Toyama, 1984a; Hara, 1986; Ota, 1986b, 1989; Toyama & Ota, 1991; Ota & Mori, 1993; Ota, 1995, 1999, 2000; Nohina et al., 1998; Yamashiro et al., 2000; Uchiyama et al., 2002; Ota et al., 2004a, b; Ota & Masunaga, 2004; Tanaka, 2004; Hoshino, 2005; Toda & Yoshida, 2005	Ota, 1994; Yamashiro & Ota, 1998
	Mexico	Y	1			Manthey & Grossmann, 1997; Röhl, 2002	
	New Zealand	N	14	Cargo stowaway (14)		McCann, 1955; Sharell, 1966; Robb, 1973, 1986; West, 1979; Gill et al., 2001	
	Nicaragua	Y	1	Cargo stowaway	Early 1970s	Henderson et al., 1976; Villa, 1993; Köhler, 1999	
	Palau	Y	1			Crombie & Pregill, 1999	Moritz et al., 1993; Hanley et al., 1995; Goldberg & Burse, 2002b

Panama	Y	1	Cargo stowaway	1916–1924	H.M. Smith & Grant, 1961; Peters & Donoso-Barros, 1970; Auth, 1994; Jaramillo et al., 1994; Rueda-Almonacid, 1999
Peru	Y	1			Ineich, 1999
Surinam	Y	1			Bauer et al., 2007
Taiwan	Y	1			Ota, 1986b, 1989, 2000; Cheng, 1987b; Lue et al., 2003
US: California	N	1	Zoo trade	1944	Shaw, 1946
US: Florida	?	2	Pet trade (2)		Meshaka et al., 2004a
US: Hawaii	Y	1	Cargo stowaway	\$400	Stejneger, 1899; Fowler, 1914; Tinker, 1938; Fisher, 1948; Oliver & Shaw, 1953; Hunsaker & Breese, 1967; Lazell, 1989b; McKeown, 1996
					Snyder, 1917; La Rivers, 1948; Baldwin et al., 1952; McMorris, 1970; Cuellar & Kluge, 1972; Quay, 1974; R.E. Jones et al., 1978, 1979; Werner, 1980, 1990a, b; Cuellar, 1984; Jarecki & Lazell, 1987; S.G. Brown & Sakai, 1988; Huey et al., 1989; Moritz et al., 1993; Petten et al., 1993; Case et al., 1994; Hanley et al., 1995, 1998; S.G. Brown et al., 1991, 1995, 1998, 2002; S.G. Brown & Duffy, 1992; S.G. Brown & O'Brien, 1993; S.G. Brown & Murphy-Walker, 1996; Burseley & Goldberg, 1996b; Petren & Case, 1996, 1998; Goldberg & Burseley, 1997; Decker et al., 2003; Wilimhoff et al., 2003

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Leposternon microcephalum</i>	US; Wisconsin Brazil: Fernando de Noronha	N N	1 1	Cargo stowaway	1958	H.M. Smith & Grant, 1961 Vanzolini, 1978	
<i>Liolaemus wiegmannii</i>	Ascension Island	Y	1			Loveridge, 1959; Ashmole & Ashmole, 1997, 2000	
<i>Lipinia noctua</i>	Cook Islands Fiji French Polynesia: Society Islands Marquesas New Zealand Tuamotu Islands US; Hawaii	Y Y Y Y Y N Y Y	1 1 1 1 1 1 1 1	Cargo stowaway Cargo stowaway Cargo stowaway	1958 1958 1958 1958 1958 1958 1958 1958	C.C. Austin, 1999 Gill et al., 2001 C.C. Austin, 1999 C.C. Austin, 1999 Hallowell, 1861; Stejneger, 1899; Tinker, 1938; Oliver & Shaw, 1953; Hunsaker & Breese, 1967; McMorris, 1970; Lazell, 1986; McKeown, 1996; C.C. Austin, 1999 C.C. Austin, 1999 Gill et al., 2001 C.C. Austin, 1999 Hallowell, 1861; Stejneger, 1899; Tinker, 1938; Oliver & Shaw, 1953	
(syn: <i>Leiopisma noctua</i> , <i>Lygosoma vertebrate</i>)							
<i>Lophognathus temporalis</i>	Vanuatu	Y	1			C.C. Austin, 1999	
<i>Lygodactylus capensis</i>	Indonesia: Biak South Africa	Y Y	1 6	Intentional Cargo stowaway (1), nursery trade (2)	1993 1981, early 2000s (2)	Günther & Kapisa, 2003 Branch, 1981, 1987; Brooke et al., 1986; Branch & Braeck, 1987; de Villiers, 2006b	
<i>Lygodactylus chobitensis</i>	Zimbabwe	Y	1			Broadley & Wilson, 2005	
<i>Lygosoma bowringii</i>	Christmas Island	Y	1			Cogger et al., 1983a; Cogger, 1992	

(syn: <i>Riopa bowringi</i>)	New Zealand	N	1	Cargo stowaway	Late 1970s	Gill et al., 2001
	Philippines	Y	2	Cargo stowaway		C.A. Ross, 1989
<i>Mabuya agilis</i>	Canary Islands	N	1			Mertens, 1934
<i>Mabuya aurata</i>	Eritrea	Y	1			Arnold, 1986
	Oman	Y	1			Arnold, 1986
	United Arab Emirates	Y	1			Soorae & Al Hameiri, 2005
<i>Mabuya carinata</i>	Maldiv Islands	?	1			W.W.A. Phillips, 1958
<i>Mabuya comorensis</i> (syn: <i>Mabuya maculilabris</i>)	Madagascar	Y	1	Cargo stowaway		Koller, 1993; Glaw & Vences, 1994; Köhler et al., 1997; Nussbaum et al., 1999; Andreone et al., 2003; Raselimanana & Vences, 2003
<i>Mabuya cunningi</i>	Taiwan	Y	1			Lue et al., 2003
<i>Mabuya multifasciata</i>	Guam	N	1	Cargo stowaway	1999	Wiles, 2000
	Taiwan	Y	1			Ota et al., 1994b
	US: Florida	Y	2	Pet trade (2)	1980s (1)	Meshaka, 1999b; Meshaka et al., 2004a
<i>Mabuya quinquetraeniata</i>	Egypt	Y	1	Nursery trade		Nešas & Vgasova, 2004
<i>Mabuya</i> sp.	Great Britain	N	1	Cargo stowaway	1960s	Yalden, 1965
	Guam	N	1	Cargo stowaway	1970	Wiles, 2000
	Madeira	N	1	Cargo stowaway		Báez & Bischoit, 1993
<i>Mediodactylus kotschy</i> (syn: <i>Cyrtodactylus kotschy</i> , <i>Cyrtopodion kotschy</i> , <i>Cyrtopodium kotschy</i>)	Hungary	Y	2	Intentional (2)	Early 1980s, 1985	Farkas et al., 1999

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>(syn: Cyrtodactylus kotschy)</i>	Italy	Y	1	Cargo stowaway		Peracca, 1905; Mertens, 1961; Bruno, 1980b; Picariello & Scillitani, 1988; Fattizzo, 1996; Grillenzoni & Mazzotti, 1999	Pozio et al., 1983
<i>(syn: Cyrtodactylus kotschy)</i>	Malta	?	1			C. Lever, 2003	
<i>Nactus</i> sp. (<i>syn: Cnemaspis kendalli</i>)	New Zealand	N	1	Cargo stowaway	1949	McCann, 1955; Robb, 1973, 1986; West, 1979; Gill et al., 2001	
<i>Oedura rhombifer</i>	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Ophisaurus apodus</i>	Austria	N	1			Eiselt, 1961	
	Germany	N	1	Pet trade		Geiger & Waitzmann, 1996	
	US: New Jersey	N	1	Intentional	§1964	Rothman, 1965	
<i>Ophisaurus ventralis</i>	Cayman Islands	?	1	Cargo stowaway	1987	Schwartz & Henderson, 1991; Seidel & Franz, 1994	
<i>Phelsuma astriata</i>	Seychelles	?	2	Cargo stowaway (2)	2004 (1)	Van Heygen, 2004	
<i>Phelsuma cepediana</i>	Madagascar	Y	2	Cargo stowaway, intentional	1962	Mertens, 1963; Raxworthy & Nussbaum, 1993; Raselimanana & Vences, 2003	
	Réunion	Y	1	Nursery trade	1960s	Cheke, 1975, 1987; Bour & Moutou, 1982	
<i>Phelsuma dubia</i>	Rodrigues	Y	1			J.J. Austin et al., 2004	
	Comoros	Y	1			Meirte, 2004	
	Kenya	Y	1			Meirte, 2004	
	Mozambique	Y	1			Meirte, 2004	

<i>Phelsuma guimbeaui</i>	Tanzania US: Hawaii	Y Y	1 1	Pet trade	Mid 1980s	Howell, 1981; Meirte, 2004 Kishinami & Kishinami, 1996; McKeown, 1996 Goldberg et al., 2003
<i>Phelsuma laticauda</i>	Comoros French Polynesia: Society Islands US: Hawaii	Y Y Y	1 1 1	Pet trade	1974	Meirte, 1999a, 2004 Ota & Ineich, 2006 Walsh, 1990; McKeown, 1996; Kraus, 2006 Goldberg et al., 2003; Calviño- Cancela, 2005; B.K. Chan et al., 2007
<i>Phelsuma lineata</i>	Réunion	Y	1	Intentional	1940s	Cheke, 1975, 1987; Bour & Moutou, 1982
<i>Phelsuma longinusulae</i>	Seychelles	N	2	Intentional (2), pet trade (5)	1990, early 1990s, 2002	Cheke, 1982 Krysko & Hooper, 2006
<i>Phelsuma madagas- cariensis</i>	US: Florida	Y	7			Krysko et al., 2003b, 2007b; Meshaka et al., 2004a; Krysko & Sheehy, 2005; Krysko & Daniels, 2005; Meshaka, 2006
<i>Phrynosoma cornutum</i>	US: Hawaii US: Alabama	Y Y	1 3	Intentional	1996	Kraus, 2002b Mount, 1975; Marion & Dindo, 1980; S.D. Carey, 1983; Price, 1990
	US: Arizona US: Arkansas	? ?	1 3	Pet trade (3)		Price, 1990 Yarrow, 1882; Dellinger & Black, 1938; Dowling, 1957
	US: California	N	2	Pet trade (2)		Banta & Morafka, 1966; Bury & Luckenbach, 1976; Jennings, 1987a, 2004

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Colorado	N	6	Pet trade (6)	1872, 1911, 1919, 1935, 1957, 1964	Rodeck, 1936; Maslin, 1959; Hammerson, 1984; Livo et al., 1998 Yarrow, 1882	
	US: District of Columbia	N	1				
	US: Florida	Y	20	Pet trade (2), intentional (1)	1964, early 1960s	DeSola, 1934; Goff, 1935; Burt, 1937; Carr, 1940; Allen & Neill, 1955; W. King & Krakauer, 1966; Bartlett, 1967a; Ashton, 1976; Layne et al., 1977; Ashton & Ashton, 1985; J.B. Jensen, 1994; Bartlett & Bartlett, 1999; Meshaka et al., 2004a; Owens & Krysko, 2007	
	US: Georgia	Y	2			Martof, 1956	
	US: Hawaii	N	1	Pet trade	1955	Hunsaker & Breese, 1967	
	US: Illinois	N	3	Pet trade (3)		P.W. Smith, 1961	
	US: Indiana	?	1			Price, 1990	
	US: Kansas	?	2	Pet trade (1)	1993	Price, 1990; Collins, 1994	
	US: Kentucky	?	1			Price, 1990	
	US: Louisiana	?	1	Intentional	1918	Strecker & Frierson, 1926; Frierson, 1927; Reeve, 1952; Dundee & Rossman, 1989; Price, 1990	
	US: Maine	N	1	Pet trade	1916	Abbott, 1922	

US: Michigan	N	1		1940	D.E. Davis, 1940; Price, 1990	
US: Mississippi	?	2	Pet trade (2)	1940	F.A. Cook, 1942; Price, 1990	
US: Missouri	?	3			Anderson, 1965; Price, 1990	
US: Nebraska	?	1			Price, 1990	
US: North Carolina	Y	13	Pet trade (11)	1880, 1908, 1920s, 1923, 1929, 1930, 1932, 1935, 1940, 1941, 1942, 1970s, 1989	Gray, 1941; Brimley, 1944; Settle, 1989; E.E. Brown, 1992; Palmer & Braswell, 1995	
US: South Carolina	Y	1			Martof et al., 1980; Price, 1990	
US: Tennessee	?	1			Price, 1990	
US: Texas	?	2			Webb & Packard, 1961; Price, 1990	
US: Virginia	N	2		1950s	Yarrow, 1882; Mitchell, 1994	
US: Wyoming	?	1			Price, 1990	
<i>Phrynosoma coronatum</i>	US: California	?	1	Intentional	1894	Mearns, 1907; Jennings, 1987a
<i>Phrynosoma</i> sp.	US: Montana	N	1		1934	Harbaugh, 1935
	US: Indiana	N	2			Minton, 1972
	US: Maryland	N	1			McCauley, 1945
	US: Massachusetts	N	1	Pet trade	1943	Cardoza et al., 1993

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Phyllodactylus leei</i>	Ecuador: Galapagos Islands	Y	1			Lanza, 1982; J.W. Wright, 1983b; Hoogmoed, 1989	
<i>Phyllodactylus reissi</i> (syn: <i>Phyllodactylus darwini</i>)	Ecuador: Galapagos Islands	Y	1	Cargo stowaway	1970s	J.W. Wright, 1983b; Hoogmoed, 1989; Olmedo & Cayot, 1994	
<i>Phyllodactylus</i> sp.	Great Britain	N	1	Cargo stowaway	1960s	Yalden, 1965	
<i>Physignathus cocincinus</i>	US: Florida	N	1	Pet trade	2000s	Krysko et al., 2006	
<i>Physignathus tesuaurii</i>	Australia	Y	1	Intentional		Larwill, 1995; Low, 2003	
<i>Plicia plicata</i> (syn: <i>Tropidurus plicata</i>)	Canary Islands	Y	1	Cargo stowaway		Pleguezuelos, 2004	
<i>Podarcis filifolensis</i>	Italy: Lampedusa	?	1	Intentional		Corti et al., 2006	
<i>Podarcis tilfordi</i>	Balearic Islands	?	2			Mertens & Wermuth, 1960; Buttle, 1986; Arnold & Oveden, 2002; Pleguezuelos, 2004	
<i>Podarcis muralis</i>	Austria	Y	4	Intentional (2), spread from adjacent introduction (1)	1932, 1933	Lenner, 1936; Eiselt, 1961; Sochurek, 1978; Merwald, 1981; Cabela & Tiedemann, 1985; Gruschwitz & Böhme, 1986; Waitzmann & Sandmaier, 1990; Guillaume, 1997	
	Belgium	N	4			Parent, 1983, 1997	
	Canada: British Columbia	Y	4	Intentional (4)	1970, 1983 (2), 1986	Gregory & Gregory, 1999; Allan et al., 2000; Deichsel & Schweigert, 2004	Allan et al., 2006; Burke et al., 2007

Germany	Y	28	Intentional (4), pet trade (22)	1874, 1916, late 1930s, 1977, 1978 (3), 1980s (3), 1982, 1985–1986	von Schweizerbarth, 1908; Mertens, 1917; Mertens & Wermuth, 1960; Preywisch & Steinborn, 1977; Forman, 1981; Gruschwitz & Böhme, 1986; Eckstein & Meinig, 1989; Lenk, 1989; Waitzmann & Sandmaier, 1990; Münch, 1992; Richter, 1994; Reichling, 1995, 1996b, 1998; Geiger & Waitzmann, 1996; Meinig & Rathjen, 1996; Schlüpmann, 1996, 1997; Härtel & Plesker, 1997; Schlüpmann & Geiger, 1998; Meßer et al., 2004	Reichling, 1996a; Franke, 1999; Münch, 2001; Felke, 2005
(syn: <i>Lacerta muralis</i>) Great Britain	Y	14	Intentional (9), pet trade (1)	1932, 1933, 1937, 1954, early 1960s, 1975, 1976, 1978, 1986, 1990s	R.H.R. Taylor, 1948, 1963; M. Smith, 1951a, b; Fitter, 1959; J.F.D. Frazer, 1964; Spellerberg, 1975; C. Lever, 1977, 1980; C.A. Snell, 1981; D. Frazer, 1989; Beebee & Griffiths, 2000; Quayle & Noble, 2000; Arnold & Ovenden, 2002; Gleed-Owen, 2004; Detchsel et al., 2007	C.A. Snell, 1984

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Greece: Corfu	Y	1		1993	Hill & Mayer, 2004; Bruekers, 2006a	
	Switzerland	Y	2			Stemmler, 1967; Kramer & Stemmler, 1986; Dušej & Müller, 1997; Guillaume, 1997	
	US: Indiana	Y	1			Walker & Deichsel, 2005	
	US: Kentucky	Y	2	Intentional (1)	1988, 1998	Draud & Ferner, 1994; Deichsel & Gist, 2001; Ferner & Ferner, 2002; Ferner, 2004	
	US: New Jersey	N	1	Cargo stowaway	1940s	Conant, 1945	
	US: Ohio	Y	2	Intentional (2)	1951, 1958	Vigle, 1977; Hedeen, 1984, 1988; Hedeen & Hedeen, 1999; Deichsel & Gist, 2001; Schweiger & Deichsel, 2003; Ferner, 2004	Kwiat & Gist, 1987; Claussen et al., 1990; R.M. Brown et al., 1995; Burke et al., 2002, 2007; Gribbens & Gist, 2003
<i>Podarcis pityusensis</i> (syn. <i>Lacerta lilfordi</i> <i>pityusensis</i>)	Balearic Islands	Y	2	Cargo stowaway (2)	>1878, 1980s	Müller, 1927; Eisentraut, 1950a, b; Alcover, 1979; Alcover & Mayol, 1981; Salvador, 1986; U. Fritz, 1992; Mayol, 1993, 2003; Rivera & Arribas, 1993; Cirer & Martínez Rica, 1997; Mateo, 1997a; Pleguezuelos, 2004	Böhme and Eisentraut, 1981; Bruekers, 1995
	Germany	N	3				
	Portugal	Y	1	Pet trade (3)	1970s (3)	Eckstein & Meimig, 1989 Arnold & Ovenden, 2002	

(syn: <i>Podarcis sicula</i>) Spain	Y	2	Intentional	1980s, 1990s	Carretero et al., 1991; Rivera & Arribas, 1993; Llorente et al., 1995; Cirer & Martínez Rica, 1997; Mateo, 1997a; Salazar Alonso, 1997, 1998; García-Porta et al., 2001; Societat Catalana d'Herpetologia, 2001; Pleguezuelos, 2004	Carretero et al., 1995
<i>Podarcis sicula</i> (syn: <i>Lacerta serpa</i>)	N	1	Intentional	1958	Deichsel & Gist, 2001	Hicks, 1992; Pérez-Mellado & Corti, 1993; Bruekers, 1997; Podnar et al., 2005
	Y	1	Cargo stowaway		Müller, 1905; Eisentraut, 1950a, b; Prats, 1980; Alcover & Mayol, 1981; Kotsakis, 1981; Esteban et al., 1994; Olmedo, 1997; Pérez-Mellado et al., 2000; Mayol, 2003; Mateo, 1997a; Pleguezuelos, 2004	
(syn: <i>Lacerta Serpa sicula</i>)	Y	3	Nursery trade	2002	Mourgue, 1924; Knoepffler, 1961; Orsini, 1984; Fretey, 1986; Michelot, 1989; Bruekers, 2003b; Martijn, 2006; Pascal et al., 2006	
	Y	2	Cargo stowaway (2)	<1877	Mertens, 1957; Lanza, 1983a, 1988; Fretey, 1986; Michelot, 1989; Cheylan & Michelot, 1992; Pascal et al., 2006	B. Schneider, 1972; Van Damme et al., 1990; Capula, 1994a; Vanhooydonck et al., 2000

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Germany	N	2	Intentional, pet trade	1913	Trautman, 1924; Geiger & Niekisch, 1983; Henle & Klaver, 1986; K. Fritz, 1987; Geiger & Wäitzmann, 1996; Klötzli & Rosenmayr, 2000	
(syn: <i>Lacerta muralis campestris</i>)	Great Britain	N	2	Intentional (2)	1954, 1961	J.F.D. Frazer, 1964; C. Lever, 1977; Henle & Klaver, 1986	
	Italy	Y	1	Nursery trade		Bruckers, 2006b	
	Italy (offshore islands)	Y	2			Lanza, 1973; Capula, 1994a, 1994b; Corti et al., 1996	Capula et al., 1987, 2002; Capula, 1992, 1993; Capula & Ceccarelli, 2003
	Italy: Lampedusa	Y	1	Cargo stowaway	1990s	Lo Valvo & Nicolini, 2001	
	Italy: Sardinia	Y	1			Lanza, 1983a; Podnar et al., 2005	
	Libya	Y	1			Arnold & Burton, 1978; Henle & Klaver, 1986	
	Portugal	?	1	Cargo stowaway		Ferrand de Almeida et al., 2001; González de la Vega et al., 2001	
	Spain	Y	4		1870s, 1960s	Mertens & Wermuth, 1960; Lanza, 1973; Meijide, 1981, 1985; Henle & Klaver, 1986; Pérez de Ana, 1996; Mateo, 1997a; Olmedo, 1997; Barbadillo et al., 1999; Diego-Rasilla et al., 2001; Pleguezuelos, 2004	Mellado & Olmedo, 1984, 1992; Olmedo et al., 1984

Switzerland	Y	7	Cargo stowaway (4), international (1), zoo trade (2)	1980s, 1987	Stemmler, 1967, 1971; Hohl, 1986; Kramer & Stemmler, 1988; Hofer & Dušej, 1995; Klötzli & Rosenmayr, 2000
Turkey	Y	1			Mertens, 1961; Lanza, 1973; Henle & Klaver, 1986; Böhme, 2000; Arnold & Burton, 2002
US: Kansas	Y	1	Pet trade	1950s	Collins, 1993; Taggart, 2004
US: New York	Y	1	Pet trade	1969	Collins, 1997; Gubanyi, 2001, 2003; Oliverio et al., 2001; L.L. Miller, 2004, 2005; Burke et al., 2007
(syn: <i>Lacerta melisellenis</i> , <i>Lacerta sicula</i>)	N	1	Pet trade	1927	Gossweiler, 1975; Garber, 1985; Alvey, 1993
<i>Pogona barbata</i> (syn: <i>Amphibolurus barbatus</i> , <i>Pogona barbatus</i>)	N	1	Pet trade		Oliverio et al., 2001; Burke & Mercurio, 2002; Burke et al., 2002, 2007; Burke & Ner, 2005; Mendyk, 2007a, b
<i>Psammodromus algirus</i>	?	1			Kaufeld, 1931; Conant, 1959; McCoy, 1982; Burke & Ner, 2005
<i>Psammodromus hispanicus</i>	Y	2			Heatwole, 1978; Limpus et al., 1999
<i>Pseudocordylus microlepidotus</i>	N	1		1886	Mastius, 1999; Pleguezuelos, 2004
<i>Ptychozoon lionotum</i>	?	1	Pet trade	2003	Bons & Geniez, 1996; Pleguezuelos, 2004
					Fitter, 1959
					Enge et al., 2004a; Krysko et al., 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Pyodactylus haselquistii</i>	US: Florida	N	1	Pet trade	1994	Bartlett, 1994b; Meshaka et al., 2004a	
<i>Pygopus lepidopodus</i>	New Zealand	N	1	Cargo stowaway	1921	W.R.B. Oliver, 1921; West, 1979	
<i>Saprosincus challengeri</i> (syn: <i>Lampropholis challengeri</i> , <i>Leiopisma chalcengeri</i>)	New Zealand	N	1	Cargo stowaway		McCann, 1955; Robb, 1973, 1986; West, 1979; Gill et al., 2001	
<i>Saprosincus mustelina</i>	Australia	Y	1	Nursery trade		Low, 2003	
(syn: <i>Lampropholis mus-telina</i> , <i>Leiopisma mustelina</i>)	New Zealand	N	1	Cargo stowaway	1952	McCann, 1955; Robb, 1973, 1986; West, 1980	
<i>Sauromalus hispidus</i>	Mexico: Sea of Cortez islands	Y	5	Food (5)	1920s	Shaw, 1946b; Case, 1982; Grismer, 1994b, 2002a; Petren & Case, 1997; Mellink, 2002; Nabhan, 2002, 2003	
<i>Sauromalus varius</i>	Mexico: Sea of Cortez islands	Y	2	Food (2)	1920s	Lowe & Norris, 1955; Case, 1982; Grismer, 1994b, 2002a; Hollingsworth et al., 1997; Petren & Case, 1997; Mellink, 2002; Nabhan, 2002, 2003	
<i>Scelarcis perspicillata</i> (syn: <i>Lacerta perspicillata</i> , <i>Podarcis perspicillata</i> , <i>Triton perspicillata</i>)	Balearic Islands	Y	1	Cargo stowaway	Early 1920s	Mertens, 1924, 1929; Eisenraut, 1950a, b; Alcover & Mayol, 1981; Kotsakis, 1981; Richter, 1986b; Esteban et al., 1994; Mateo, 1997a, b; Mayol, 2003; Pleguezuelos, 2004	Hicks, 1992; Bruekers, 1997; Harris et al., 2003; Perera et al., 2006

(syn: <i>Podarcis perspicillata</i>)	Spain	?	1			Richter, 1986b
<i>Sceloporus jarrovi</i>	US: California	N	1	1970s		Jennings, 1987a, 2004
<i>Sceloporus magister</i>	US: Florida	N	1	1964	Pet trade	W. King & Krakauer, 1966
<i>Sceloporus occidentalis</i>	Guam	N	1	1992	Cargo stowaway	Wiles, 2000
<i>Sceloporus poinsettii</i>	US: Washington	Y	4	1986, 1990 (3)	Research (4)	H.A. Brown, 1992
<i>Sceloporus serrifer</i> (syn: <i>Sceloporus cyano-genys</i>)	US: California	N	1	1980	Pet trade	Jennings, 1987a, 2004
	US: Florida	N	1	1964	Pet trade	W. King & Krakauer, 1966
	US: California	N	1	1970	Pet trade	Stebbins, 1972; Bury & Luckenbach, 1976; Jennings, 1987a, 2004
<i>Sceloporus undulatus</i>	US: New York	Y	3	1942 (3)	Zoo trade (3)	Kaufeld, 1946, 1948, 1955; Garber, 1985; Feinberg, 2004
<i>Scincella lateralis</i>	US: Wisconsin	N	1	1973	Intentional	R.C. Vogt, 1981
scincid sp.	New Zealand	N	1		Cargo stowaway	Gill et al., 2001
	New Zealand	N	2		Cargo stowaway (2)	Gill et al., 2001
<i>Sphaerodactylus argus</i>	Bahamas	Y	1		Cargo stowaway	Barbour, 1937; Schwartz, 1968b; R. Thomas, 1975
	Cuba	Y	1			Barbour, 1937; Savage, 1954; Buiide, 1967; R. Thomas, 1975; Estrada & Ruibal, 1999
	Honduras	Y	1			Schwartz, 1973
	Mexico: Yucatán	Y	1	1974		Harris & Kluge, 1984; Flores-Villela, 1993; J.C. Lee, 1996, 2000
	Panama	Y	1			Harris & Kluge, 1984; Auth, 1994; Savage, 2002; Köhler, 2003

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US; Florida	Y	1	Cargo stowaway	Early 1940s	Savage, 1954; W. King & Krakauer, 1966; Love, 1978; L.D. Wilson & Porras, 1983; Lawson et al., 1991; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Krysko & King, 2002c; Meshaka et al., 2004a; Krysko & Daniels, 2005; Krysko & Sheehy, 2005	
<i>Sphaerodactylus copei</i>	Bahamas	Y	1	Cargo stowaway		Schwartz, 1968b; Franz et al., 1996; D.S. Lee, 2004, 2005	
<i>Sphaerodactylus elegans</i> (syn: <i>Sphaerodactylus cinereus</i>)	US; Florida	Y	1	Cargo stowaway		Stejneger, 1922; Burt, 1937; Carr, 1940; Allen & Slatten, 1945; Mittleman, 1950; Duellman & Schwartz, 1958; W. King & Krakauer, 1966; L.D. Wilson & Porras, 1983; Epler, 1986; Ashton & Ashton, 1988; Lazell, 1989a; Lawson et al., 1991; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2004a; Krysko & Daniels, 2005; Krysko & Sheehy, 2005	Krysko et al., 2003c
<i>Sphaerodactylus glaucus</i>	US; Kentucky	N	1	Cargo stowaway	1928	W.R. Allen, 1928	

<i>Sphaerodactylus lineolatus</i>	US: Alabama	N	1			Intentional	1960s	Mount, 1975
<i>Sphaerodactylus macrolepis</i>	US: Florida	N	1			Intentional	1960s	W. King & Krakauer, 1966
<i>Sphaerodactylus microlepis</i>	Dominica	?	1					Evans, 1989; Malhotra & Thorpe, 1999
<i>Sphaerodactylus notatus</i>	Bahamas	?	1					Schwartz, 1965, 1970, 1973
	Jamaica: Morant Cays	?	1					Schwartz, 1965, 1970, 1973
	US: Alabama	N	1				1900	Burt, 1937
<i>Sphaerodactylus</i> sp.	US: Indiana	N	1			Cargo stowaway		Minton, 1972
<i>Tarentola annularis</i>	US: Florida	Y	3			Pet trade (3)	1990	Bartlett & Bartlett, 1999; Meshaka et al., 2004a; Krysko & Daniels, 2005
<i>Tarentola boettgeri</i>	Spain	?	6			Cargo stowaway (6)		Pleguezuelos, 2004
<i>Tarentola delalandii</i>	Great Britain	N	1			Cargo stowaway		Fitter, 1959
	Spain	N	2			Cargo stowaway (2)		J. Rivera & Arribas, 1993; Pleguezuelos, 2004
<i>Tarentola mauritanica</i>	Argentina	Y	1			Cargo stowaway	1963	Castello & Gil Rivas, 1980; Joger, 1984a; Navas, 1987; Cei, 1993; Cabrera & Guerra, 2006
	Balearic Islands	Y	1					Alcover & Mayol, 1981; Balcells, 1955b; Salvador, 1978, 1993; Mayol, 1992; Roca, 1993; Bruckers, 1997 Kotsakis, 1981; J. Rivera & Arribas, 1993; Esteban et al., 1994; Palerm, 1997; Mayol, 2003; Harris et al., 2004a, b; Pleguezuelos, 2004

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Bolivia	?	1			Montero et al., 1995	
	Canary Islands	Y	1			Joger, 1984a; Bischoff, 1985	
	France	Y	11	Cargo stowaway (2), vehicle	1995, 2000, 2001	Fretey, 1986; Geniez, 1989; Defos du Rau & Crochet, 1994; Martínez Rica, 1997; Noblet, 2003; Pascal et al., 2006	
	Germany	N	1	Pet trade	1981	Eckstein & Meinig, 1989	
	Great Britain	N	1	Intentional		J.F.D. Frazer, 1964	
	Greece	Y	1			Rieppel, 1981; Joger, 1984a	
	Greece: Crete	Y	1			Rieppel, 1981; Harris et al., 2004a, b	Arad et al., 1997
	Italy	Y	4	Nursery trade (1)		Bennati et al., 1975; Rieppel, 1981; Lapini et al., 1996; Caldonazzi et al., 2002; Harris et al., 2004a, b; Bruckers, 2006	
	Madeira	Y	1		1980s	Báez & Biscoito, 1993; Ferrand de Almeida et al., 2001; Jesus et al., 2002; Harris et al., 2004a, b	Nogales et al., 1998; Carranza et al., 2000
	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
	Portugal	Y	1			Harris et al., 2004a, b	

Spain	Y	3			Barbadillo et al., 1999; Harris et al., 2004a, b; Pleguezuelos, 2004
Turkey	Y	1			Cyren, 1935; Joger, 1984a
Uruguay	Y	1		Cargo stowaway	Achaval & Gudynas, 1983; Joger, 1984a; Cej, 1993
US: California	Y	1		Pet trade	Mahrdt, 1998
US: Delaware	N	1		Cargo stowaway	Conant, 1945
US: Florida	Y	3		Pet trade (3)	Bartlett & Bartlett, 1999; Meshaka et al., 2004a
US: New Jersey	N	2		Cargo stowaway (2)	Conant, 1945
Senegal	Y	1		[Cargo stowaway, vehicle]	Joger, 1980, 1984a
<i>Tarentola parvicarinata</i>					
<i>Tetra dugesii</i> (syn: <i>Lacerta dugesii</i> , <i>Podarcis dugesii</i>)	Y	1		<1860	Morelet, 1860; Drouët, 1861; Godman, 1870; Chaves, 1949; Ulfstrand, 1961; Richter, 1986a, 1998; Dellinger, 1997; Mateo, 1997a; Ferrand de Almeida et al., 2001 Malkmus, 1984; Schielzeth, 1991
(syn: <i>Lacerta dugesii</i>)	N	1		Intentional	J.F.D. Frazer, 1964
Netherlands	N	1		1989	Gubbels, 1992
Portugal	Y	1		Cargo stowaway	Sá-Sousa, 1995; Dellinger, 1997; Mateo, 1997a; Ferrand de Almeida et al., 2001
(syn: <i>Lacerta dugesii</i> , <i>Podarcis dugesii</i>)				<1992	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Tiliqua rugosa</i> (syn: <i>Trachydosaurus rugosus</i> , <i>Trachysaurus rugosus</i>)	Australia	Y	4	Intentional (2)	1926, >1902	Lord & Scott, 1924; Lord, 1927; E.R. Waite, 1927, 1929; A.J. Bartlett, 1948; Houston & Tyler, 1979; Sarre et al., 1990; Copley, 1994; Larwill, 1995	Roberts, 1964, 1969
<i>Tiliqua scincoides</i>	Australia	Y	2	Cargo stowaway, intentional	1990s, >1926	Houston & Tyler, 1979; O'Dwyer et al., 2000	
<i>Tiliqua</i> sp.	New Zealand US: California	N N	1 1	Cargo stowaway Pet trade	1930	Gill et al., 2001 G.S. Myers, 1951; Bury & Luekenbach, 1976; Jennings, 1987a, 2004	
<i>Timon lepidus</i> (syn: <i>Lacerta lepida</i>)	France Great Britain	N N	1 1	Intentional	1932	Pascal et al., 2006 Fitter, 1959; J.F.D. Frazer, 1964	
(syn: <i>Lacerta lepida</i>)	Malta	N	1	Intentional	1964	Lanfranco, 1964	
(syn: <i>Lacerta lepida</i>)	US: New Jersey	N	1	Cargo stowaway	1944	Conant, 1945	
<i>Tretioscincus bifasciatus</i>	Colombia: Isla de Providencia	?	1		1960s	Scott & Ayala, 1984; Ayala, 1986; Rueda-Almonacid, 1999	
<i>Tropidurus hispidus</i>	US: Florida	?	1	Pet trade	2003	Engel et al., 2004a	
<i>Tupinambis teguixin</i>	Brazil: Fernando de Noronha	Y	1	Biocontrol	1970s	Homewood, 1995; Hafner, 1997	
	Colombia: Isla de San Andrés	?	1			Rueda-Almonacid, 1999	

(syn: <i>Tupiaambis nigropunctatus</i>)	US: Florida	N	4	Pet trade (2)	Early 1970s, 1994	H.M. Smith & Kohler, 1978; Butterfield et al., 1997; Meshaka et al., 2004a
<i>Tupiaambis</i> sp.	US: California	N	3	Pet trade (3)		Bury & Luckenbach, 1976; Jennings, 1987a, 2004
<i>Uromastyx acanthinurus</i>	Balearic Islands	N	1			Alcover & Mayol, 1981
	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004
	Morocco	N	1	Pet trade	1990	Pleguezuelos, 2004
<i>Uta stansburiana</i>	US: California	Y	1	Cargo stowaway	1980s--1990s	Mahoney et al., 2003
<i>Varanus caudolineatus</i>	Australia	N	1	Cargo stowaway		Bush, 1987
<i>Varanus exanthematicus</i>	US: California	N	1	Pet trade	1970	Bury & Luckenbach, 1976; Jennings, 1987a, 2004
	US: Florida	N	2	Pet trade	1992, 1996	Prusak, 1992; Dalrymple, 1994; Duquesnel, 1996
<i>Varanus gouldii</i>	US: Massachusetts	N	4	Pet trade (4)	1989 (1)	Cardoza et al., 1993
	Australia	Y	1			Robinson et al., 1985; Copley, 1994
<i>Varanus indicus</i>	CNMI	Y	1			G. Fritz, 1901; von Crampton, 1921; R.P. Owen, 1974; Wiles et al., 1990; Prowazek, 1913; Wiles et al., 1989; Rodda et al., 1991; Pregill, 1998; Crombie & Pregill, 1999
	FSM	Y	2	Biocontrol, food	Early 1900s	McCoid, 1993b; McCoid & Hensley, 1993a; Wiles & Guerrero, 1996; S.R. Vogt & Williams, 2004
						H.I. Fisher, 1948; Weckler, 1949; Baies & Abbott, 1958; W.B. Jackson, 1962; Laird, 1963; Marshall, 1975; Ashby, 1983; Buden, 1995, 1996, 2000; Crombie & Pregill, 1999
						T. Uchida, 1966, 1967, 1969

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Guam	Y	1			Safford, 1905; Van Denburgh, 1917a; Dryden & Taylor, 1969; Pregill, 1998; Crombie & Pregill, 1999	Crampton, 1921; Dryden, 1965; Wikramanayake & Dryden, 1988; McCoid & Hensley, 1991, 1993a; McCoid, 1993b; McCoid & Witteman, 1993; McCoid et al., 1994a; S.R. Vogt & Williams, 2004
	Marshall Islands	Y	1			Fisher, 1948; Fosberg, 1956; Lamberson, 1987; Spennemann, 1997; Crombie & Pregill, 1999	Fulbeck, 1947
<i>Varanus niloticus</i>	Spain	N	2	Pet trade (2)	1994, 1998	Pleguezuelos, 2004	
	US: Florida	Y	2	Pet trade (2)	<1990, 1995	Dalrymple, 1994; Duquesnel, 1996; T. Campbell, 2003b, 2005; Engé et al., 2004c; Meshaka, 2006	
<i>Varanus rosenbergi</i>	US: Massachusetts	N	4	Pet trade (4)		Cardoza et al., 1993	
	Australia	Y	5		<1939, <1960	Tindale, 1924; Mirtschin, 1982, 1983; Mirtschin & Jenkins, 1985; Robinson et al., 1985; Copley, 1994	
<i>Varanus salvator</i>	Taiwan	N	1			Zhao & Adler, 1993	
	US: California	N	1	Pet trade	1978	Jennings, 1987a, 2004	
	US: Florida	N	1			Dalrymple, 1994	

<i>Zootoca vivipara</i> (syn: <i>Lacerta vivipara</i>)	Great Britain	N	1	Intentional	1930s	Fitter, 1959
(syn: <i>Lacerta vivipara</i>)	Malta	N	1	Intentional	1910s	Despott, 1913
	New Zealand	N	1	Nursery trade	1885	Kirk, 1896; Thomson, 1922; West, 1979; Robb, 1986
SNAKES						
<i>Acanthophis</i> sp.	New Zealand	N	1	Cargo stowaway		Gill et al., 2001
<i>Acrochordus javanicus</i>	US: Florida	?	1	Intentional	1980s	Loope et al., 2001; Meshaka et al., 2004a; Bartlett & Bartlett, 2005
<i>Agkistrodon piscivorus</i>	US: Colorado	N	1	Intentional	1965	Livo et al., 1998
	US: Kansas	N	1	Intentional	1970s	Collins, 1993
	US: Massachusetts	N	1		1980s	Cardoza et al., 1993
<i>Alsophis rufiventris</i>	St. Maarten	N	1		2004	Powell et al., 2005
<i>Amphiesma vibakari</i>	Japan: Izu Islands	Y	1		1968	Sengoku, 1979; M. Hasegawa & Moriguchi, 1989; M. Hasegawa, 1990, 1999; Toda & Yoshida, 2005
<i>Boa constrictor</i>	Aruba	Y	1	Pet trade	1990s	Quick et al., 2005; van Buurt, 2005, 2006
	Brazil	N	19	Pet trade (19)	1990s (19)	Eterovic & Duarte, 2002
	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004
	Chile	N	1	Cargo stowaway		Donoso-Barros, 1966
	Curaçao	N	3	Pet trade (2)		van Buurt, 2005, 2006
	Germany	N	1	Pet trade		Geiger & Waitzmann, 1996
	Guadeloupe	N	1	Intentional		Breuil, 2002
	Mexico: Cozumel	Y	1	Intentional	1971	Martínez-Morales & Cuaron, 1999
	St. Maarten	N	1	Pet trade		Powell et al., 2005

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: California	N	3	Pet trade (3)		Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
	US: Colorado	N	1	Pet trade	§1994	Livo et al., 1998	
	US: Florida	Y	3	Pet trade	1981, mid-1980s	W. King & Krakauer, 1966; Dalrymple, 1994; Butterfield et al., 1997; Meshaka et al., 2000, 2004a; Bartlett & Bartlett, 2005	Snow et al., 2007b
	US: Hawaii	N	2	Cargo stowaway, pet trade	1979, 1990s	Fritts, 1987; Kraus & Cravalho, 2001	
	US: Indiana	N	3	Cargo stowaway (2), pet trade		Minton, 1972, 2001	
(syn: <i>Boa imperator</i>)	US: Iowa	N	6	Cargo stowaway (6)	1914, 1922 (3)	Guthrie, 1923; Christiansen, 2001	
(syn: <i>Boa imperator</i>)	US: Kentucky	N	1	Cargo stowaway	1928	W.R. Allen, 1928	
	US: Maine	N	1	Cargo stowaway	1929	R.L. Lowe, 1929	
	US: Massachusetts	N	3	Pet trade (3)	1980s (3)	Cardoza et al., 1993	
(syn: <i>Boa imperator</i>)	US: Minnesota	N	1	Cargo stowaway	1890s	Guthrie, 1923	
	US: Virginia	N	1	Pet trade	1986	Mitchell, 1994	
<i>Boaedon fuliginosus</i>	Brazil	N	3	Pet trade (3)	1990s (3)	Eterovic & Duarte, 2002	
boid sp.	US: Wisconsin	N	2	Cargo stowaway (2)	1916, 1920s	Wagner, 1928	
<i>Boiga irregularis</i>	Chagos Archipelago	N	1	Cargo stowaway		Fritts, 1987; Fritts et al., 1999	
	CNMI	?	3	Cargo stowaway (3)	1987, 1990, 1991	Fritts, 1987; McCooid & Stinson, 1991; Fritts et al., 1999; Rodda & Savidge, 2007	

FSM	N	1	Cargo stowaway	1994	Fritts et al., 1999; Buden, 2000a; Buden et al., 2001	Fritts et al., 1987, 1990, 1994; Savidge, 1987b, 1988, 1991; Conry, 1988; Engbring & Fritts, 1988; Haddock et al., 1990; Fritts & McCoid, 1991, 1999; McCoid, 1991; Rodda, 1991, 1992a, b; Rodda & Fritts, 1992; Fritts & Rodda, 1995, 1998; Jordan & Rodda, 1994; Rodda et al., 1997, 1999a-c; Whittier et al., 1997; Whittier & O'Donoghue, 1998; Fritts & Chiszar, 1999; Tobin et al., 1999; Jackson & Perry, 2000; Jakes et al., 2003; Wiles et al., 2003; Vice et al., 2005; Burnett et al., 2006; Rodda & Savidge, 2007; Savidge et al., 2007; Rodda & Reed, 2008
Guam	Y	1	Cargo stowaway		Stevens, 1953; Guam, Office of the Governor, 1955; Dryden & Taylor, 1969; Savidge, 1987a; Fritts, 1988; Rodda et al., 1992	
Japan: Ryukyu Islands	N	1	[Aircraft, cargo stowaway]	1990	Ota, 1995, 1999; Katsuren et al., 1996; Fritts et al., 1999	
Marshall Islands	N	1	Aircraft stowaway	1979	Fritts et al., 1999	
New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
US: Hawaii	N	8	[Aircraft, cargo stowaway] (8)	1981 (2), 1986, 1989, 1990s, 1991 (2), 1994	Fritts, 1987; Fritts et al., 1999; Kraus & Cravalho, 2001	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Boiga irregularis</i> (?)	US: Texas Wake Island	N N	1 1	Cargo stowaway Cargo stowaway	1993 1949	McCoid et al., 1994b E.H. Bryan, 1959; Fritts et al., 1999	
<i>Bothriechis schlegelii</i> (syn: <i>Bothrops schlegelii</i>)	Chile	N	1	Cargo stowaway		Donoso-Barros, 1966	
(syn: <i>Bothrops schlegelii</i>)	US: Indiana	N	1	Cargo stowaway		Minton, 1972, 2001	
<i>Bungarus fasciatus</i>	FSM	N	1	Cargo stowaway	2002	Buden & Wichap, 2003	
<i>Calamaria</i> sp.	US: Hawaii New Zealand	N N	1 1	Cargo stowaway Cargo stowaway		Fritts, 1987 Gill et al., 2001	
<i>Candoia bibroni</i>	New Zealand	N	2	Cargo stowaway (2)	1893	Anonymous, 1893; Gill et al., 2001	
<i>Carphophis amoenus</i>	US: Massachusetts	?	1	Intentional	1977	Cardoza et al., 1993	
<i>Cerastes cerastes</i>	Spain	N	1	Pet trade	2000	Pleguezuelos, 2004	
<i>Coluber constrictor</i>	US: Hawaii	N	2	Cargo stowaway (2)	1990s (2)	Kraus & Cravalho, 2001	
colubrid sp.	New Zealand	N	4	Cargo stowaway (4)		Gill et al., 2001	
<i>Corallus annulatus</i>	Chile	N	1	Cargo stowaway		Donoso-Barros, 1966	
<i>Corallus caninus</i> (syn: <i>Boa canina</i>)	Brazil US: California	N N	5 2	Pet trade (5) Cargo stowaway (2)	1990s (5) 1922, 1932	Eterovic & Duarte, 2002 Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
<i>Corallus hortulanus</i> (syn: <i>Corallus enydris</i>)	US: California	N	3	Pet trade (3)		Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
<i>Corallus</i> sp.	US: Florida	N	1	Pet trade	1960s	Bartlett, 1967a	
<i>Crotalus adamanteus</i>	US: Maine	N	1			Palmer, 1946	

<i>Crotalus atrox</i>	US: Virginia	N	1	Snake-handling cult escapee	Š1964	Mitchell, 1994
	US: Kansas	N	14	Intentional (1), pet trade (6)	1990s (1)	H.M. Smith & Kohler, 1978; Anonymous, 2003
	US: Wisconsin	N	1			Pope, 1928; H.M. Smith & Kohler, 1978
<i>Crotalus horridus</i>	US: Maryland	N	1	Pet trade	1971	Cooper, 1960
	US: Massachusetts	N	1			Cardoza et al., 1993
<i>Crotalus scutulatus</i>	US: Kansas	N	1		1980	Collins, 1993; Anonymous, 2003
<i>Crotalus viridis</i>	US: California	Y	1			Storer, 1933a
	US: Colorado	N	1	Pet trade	1993	Livo & Chiszar, 1994
	US: Iowa	N	1	Pet trade	1991	Christiansen, 2001
	US: Kansas	N	1			H.M. Smith & Kohler, 1978; Conant & Collins, 1998
<i>Dendrelaphis caudolineatus</i>	US: Massachusetts	N	1		1989	Cardoza et al., 1993
	CNMI	N	1	Cargo stowaway	1989	McCoid & Stinson, 1991
<i>Dendrelaphis punctulatus</i>	Australia	N	1	Cargo stowaway	1996–1997	Limpus et al., 1999
	New Zealand	N	1	Cargo stowaway		Gill et al., 2001
<i>Dendrelaphis</i> sp.	FSM	N	1	Cargo stowaway	1980s	Fritts et al., 1999; Buden, 2000a; Buden et al., 2001
<i>Diadophis punctatus</i>	Cayman Islands	?	1	Cargo stowaway	1987	Schwartz & Henderson, 1991; Seidel & Franz, 1994
	Curaçao	N	1	Nursery trade		van Buurt, 2005
	US: Hawaii	N	1		1990s	Kraus & Cravalho, 2001

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Dinodon rufizonatum</i>	Japan; Ryukyu Islands	?	2		1987, 1990	Ota, 1995, 1999; Katsuren et al., 1996	
<i>Dolichophis jugularis</i> (syn: <i>Coluber jugularis</i>)	Great Britain	N	1	Pet trade		J.F.D. Frazer, 1964	
<i>Drymarchon corais</i>	Chile	N	1	Cargo stowaway		Donoso-Barros, 1966	
	US: California	N	1	Pet trade	1969	Bury & Luckenbach, 1976; Jennings, 1987a, 2004; P.R. Brown, 1997	
	US: Idaho	N	1	Pet trade	1928	Erwin, 1928	
<i>Elaphe carinata</i>	Japan; Ryukyu Islands	?	1		1989	Ota, 1995, 1999; Katsuren et al., 1996	
<i>Elaphe climacophora</i>	Japan; Izu Islands	Y	1			M. Hasegawa, 1999	Moriguchi & Hasegawa, 1982
<i>Elaphe guttata</i>	Anguilla	N	1	Cargo stowaway		Hodge et al., 2003	
	Antigua	N	1			Powell & Henderson, 2003	
	Bahamas	Y	1	Nursery trade	1993	Buckner & Franz, 1994c; D.S. Lee, 2004, 2005	
	Bonaire	N	1		2002	Perry et al., 2003; van Buurt, 2005, 2006	
	Brazil	N	3	Pet trade (3)	1990s (3)	Eterovic & Duarte, 2002	
	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	
	Cayman Islands	Y	1	Nursery trade	1985	Franz et al., 1987; Schwartz & Henderson, 1991; Seidel & Franz, 1994	
	Curaçao	N	3	[Nursery trade, pet trade] (3)	2001, 2002, 2003	Perry et al., 2003; van Buurt, 2006	

Germany	N	5	Pet trade (5)	1980s (5)	Münch, 1992; Geiger & Waitzmann, 1996
Spain	N	3	Pet trade (3)	1996, 1997, 2001	Pleguezuelos, 2004
St. Barts	N	1	Nursery trade	1996	Breuil, 2002; Hodge et al., 2003
St. Maarten	N	1			Powell et al., 2005
U.S. Virgin Islands	?	1	Cargo stowaway	1990s	Hodge et al., 2003; Perry et al., 2003; Platenberg & Boulton, 2006
US: California	N	2	Cargo stowaway, pet trade	1935	Jennings, 1987a, 2004; P.R. Brown, 1997
US: Colorado	N	1	Cargo stowaway	§1976	Livo et al., 1998
US: Hawaii	N	1	Pet trade	1990s	Kraus & Cravalho, 2001
US: Massachusetts	N	1	Nursery trade	1980–1981	Cardoza et al., 1993
Bahamas	N	1	Nursery trade	1992	Buckner & Franz, 1994d; D.S. Lee, 2004, 2005
Brazil	N	1	Pet trade	1990s	Eterovic & Duarte, 2002
Great Britain	N	1	Pet trade	1986	Young, 1987
US: Maryland	N	3	Intentional (1), pet trade (2)	1928, 1930	Mansueti, 1941a; McCauley, 1945
US: Massachusetts	N	2	Pet trade	1988, 1990	Cardoza et al., 1993
US: North Carolina	N	1	Pet trade	1941	Brimley, 1944; Palmer & Braswell, 1995
New Zealand	N	1	Cargo stowaway		Gill et al., 2001
Balearic Islands	Y	1		§5000 BC	Alcover & Mayol, 1981; Kotsakis, 1981; Esteban et al., 1994; Mateo, 1997a; Pleguezuelos, 2004

Elaphe obsoleta

Elaphe quadrivirgata

Elaphe scalaris

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Elaphe situla</i>	Italy	N	1			Razzetti & Sindaco, 2006	
	Germany	N	1	Pet trade		Geiger & Waitzmann, 1996	
<i>Elaphe taeniura</i>	Japan; Ryukyu Islands	Y	2	Pet trade	1950s, 1985	Otani & Terada, 1993; Otani, 1995, 1998; Sasaki, 1995; Ota, 1995, 1999, 2000; Katsuren et al., 1996; Ota et al., 2004a; Toda & Yoshida, 2005	
	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Elaphe</i> sp.	Brazil	N	2	Pet trade (2)	1990s (2)	Eterovic & Duarte, 2002	
<i>Epicrates cenchrina</i>	Brazil	N	9	Pet trade (9)	1990s (9)	Eterovic & Duarte, 2002	
	Chile	N	1	Cargo stowaway		Donoso-Barros, 1966	
<i>Epicrates</i> sp.	Surinam	?	1	Pet trade	1976	Hoogmoed, 1981	
<i>Eumeces murinus</i>	US: Florida	N	1			Dalrymple, 1994	
<i>Eumeces notaeus</i>	US: Florida	N	1			Dalrymple, 1994	
<i>Eumeces</i> sp.	US: Florida	N	2	Pet trade, intentional	1960s	Bartlett, 1967a; Franke & Telecky, 2001	
<i>Hemorrhois algirus</i> (syn: <i>Coluber algirus</i>)	Malta	Y	1	Cargo stowaway	1910s	Borg, 1939; Lanfranco, 1955, 1964; Mertens, 1968b; Schembri, 1984; Savona-Ventura, 1985; Lanza, 1987; Lang, 1993; Lanza & Corti, 1993, 1996; Jøger, 1997	
<i>Hemorrhois hippocrepis</i> (syn: <i>Coluber hippocrepis</i>)	Italy: Sardinia	Y	1			Bruno & Hotz, 1976; Honegger, 1978; Lanza, 1983a; Böhme, 2000	Corti et al., 2000

<i>Heterodon nasicus</i>	US: Hawaii	N	1	Cargo stowaway	1990s	Kraus & Cravalho, 2001
<i>Hierophis viridiflavus</i> (syn: <i>Coluber viridiflavus</i>)	Belgium	N	2	Pet trade (2)		de Wavrin, 1974; Parent, 1981, 1983; Percsy, 1998
(syn: <i>Coluber viridiflavus</i>)	Greece	Y	1			Utiger & Schätti, 2004
(syn: <i>Coluber viridiflavus</i>)	Switzerland	Y	6	Cargo stowaway (3), international (3)	1945, 1955	Pillet & Gard, 1979; Hotz & Broggi, 1982; Kramer & Stemmler, 1986, 1988; Heimes, 1993; A. Keller et al., 1993; Geiger & Waitzmann, 1996; Pillet, 1996
<i>Homoroselaps lacteus</i> (syn: <i>Elaps lacteus</i>)	South Africa	N	1	Cargo stowaway		Hewitt & Power, 1913; Siegfried, 1962; Brooke et al., 1986; Marais, 1992
<i>Imantodes cenchoa</i>	US: Indiana	N	1	Cargo stowaway		Minton, 1972
<i>Imantodes</i> sp.	Curaçao	N	2	Cargo stowaway (2)		van Buurt, 2005
<i>Lampropeltis alterna</i>	US: Florida	N	1	Pet trade	1995	Duquesnel, 1996
	US: Hawaii	N	1	Pet trade	1990s	Kraus & Cravalho, 2001
<i>Lampropeltis calligaster</i>	US: Pennsylvania	N	1	Pet trade	1902	McCoy, 1982
<i>Lampropeltis getula</i>	Brazil	N	7	Pet trade (7)	1990s (7)	Eterovic & Duarte, 2002
	Canary Islands	N	1	Pet trade	1990s	Pleguezuelos, 2004; Pether & Mateo, 2007
	Great Britain	N	1		1987	Young, 1988
	US: California	N	1	Pet trade	1970	Bury & Luckenbach, 1976; Jennings, 1987a, 2004; P.R. Brown, 1997

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Hawaii	N	2	Pet trade (2)	1990s (2)	Kraus & Cravalho, 2001	
	US: Massachusetts	N	2	Pet trade (1)	1969, 1979	Lazell, 1976; Cardoza et al., 1993	
	US: Virginia	N	1	Pet trade	1946	Linzey & Clifford, 1981	
<i>Lampropeltis triangulum</i>	Brazil	N	1	Pet trade	1990s	Eterovic & Duarte, 2002	
(syn: <i>Cornella doliaia</i>)	Great Britain	N	1	Pet trade	~1809	Fitter, 1959	
US: California	N	1	Pet trade			P.R. Brown, 1997	
US: Indiana	N	1	Cargo stowaway			Minton, 1972	
US: Massachusetts	N	1	Nursery trade		1988	Cardoza et al., 1993	
<i>Lampropeltis</i> sp.	Brazil	N	2	Pet trade (2)	1990s (2)	Eterovic & Duarte, 2002	
<i>Lamprophis fuliginosus</i>	US: California	N	1	Pet trade		P.R. Brown, 1997	
<i>Laticauda colubrina</i>	Greece: Corfu	N	1		1985	Steinicke & Trutnau, 1993; Tóth et al., 2002	
<i>Leioheterodon madagas-</i> <i>carisensis</i>	Comoros	Y	1	Biocontrol	Early 1900s	Wallach, 1986; Meirte, 1993, 2004; Raselimanana & Vences, 2003	
<i>Leiopython albertisii</i>	Brazil	N	1	Pet trade	1990s	Eterovic & Duarte, 2002	
(syn: <i>Liasis albertisii</i>)							
<i>Leptodeira annulata</i>	Chile	N	1	Cargo stowaway		Donoso-Barros, 1966	
	US: California	N	3	Cargo stowaway (3)	<1966	Banta & Morafka, 1966; Jennings, 1987a, 2004	
	US: Colorado	N	2	Cargo stowaway (2)	1958, 1967	Livo et al., 1998	
<i>Leptodeira</i> sp.	Curaçao	N	3	Cargo stowaway (3)		van Buurt, 2005	

	US: Indiana	N	2	Cargo stowaway (2)		Minton, 1972, 2001
<i>Leptophtis abbaetulla</i>	Chile	N	1	Cargo stowaway		Donoso-Barros, 1966
<i>Leptophtis depressirostris</i>	Great Britain	N	3	Cargo stowaway (3)	1960s (3)	Yalden, 1965
<i>Leptotyphlops albifrons</i>	Bonaire	Y				van Buurt, 2005, 2006
<i>Leptophtis</i> sp.	Curaçao	N	1	Cargo stowaway		van Buurt, 2005
<i>Lycodon antileus</i>	Christmas Island	Y	1	Cargo stowaway	1987	L.A. Smith, 1988; Fritts, 1993; Cogger, 1992
	FSM	N	1	Cargo stowaway	1986	Fritts, 1987; Buden, 2000a; Buden et al., 2001
	Indonesia: Sulawesi	Y	1	Cargo stowaway		Leviton, 1965; Fritts, 1993
	Indonesia: Timor	Y	1	Cargo stowaway		Leviton, 1965; Fritts, 1993
	Mauritius	Y	1		1870s	Koenig, 1932; Blanc, 1972; C.G. Jones, 1993 Cheke, 1987; Henkel & Schmidt, 1995
	New Zealand	N	1	Cargo stowaway		Gill et al., 2001
	Philippines	Y	1	Cargo stowaway		Leviton, 1965
	Réunion	Y	1	Cargo stowaway	<1839	Maillard, 1862; Mertens, 1934; Blanc, 1972; Bour & Moutou, 1982; Cheke, 1987
<i>Lystrophis dorbignyi</i>	Brazil	N	1	Pet trade	1990s	Eterovic & Duarte, 2002
<i>Lystrophis semicinctus</i>	Brazil	N	1	Pet trade	1990s	Eterovic & Duarte, 2002

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Macroprotodon cucullatus</i>	Balearic Islands	Y	1		~200 BC	Eisenbraut, 1950a, b; Alcover & Mayol, 1981; Kotsakis, 1981; Busack & McCoy, 1990; Mayol, 1993; Esteban et al., 1994; Mateo, 1997a; Pleguezuelos, 2004	Buttle, 1991; Pleguezuelos et al., 1994
<i>Malpolon monspes-sulanus</i>	Slovenia	?	1			Tome, 1997	
	US: Pennsylvania	N	1	Cargo stowaway	1943	Dillon, 1944	
<i>Masticophis flagellum</i>	US: New Jersey	N	1	Intentional	~1964	Rothman, 1965	
<i>Micrurus fulvius</i>	Curaçao	N	1	Nursery trade		van Buurt, 2005	
	US: Indiana	N	1		1889	Bigney, 1892; Butler, 1892; Hay, 1892; Link, 1951; Minton, 1972	
	US: Ohio	N	2		~1880s, 1944	Conant, 1951; Link, 1951	
	US: Pennsylvania	N	1	Cargo stowaway		Conant, 1951	
<i>Morelia spilota</i>	Australia	N	1	Cargo stowaway	1990s	O'Dwyer et al., 2000	
<i>Morelia viridis</i>	Australia	N	1	Cargo stowaway	1990s	O'Dwyer et al., 2000	
<i>Naja haje</i>	US: California	N	1	Pet trade	1970	Bury & Luckenbach, 1976; Jennings, 1987a, 2004; P.R. Brown, 1997	
	US: Florida	N	1	Religious	Early 1970s	L.D. Wilson & Porras, 1983	
<i>Naja kaouthia</i> (syn: <i>Naja sp.</i>)	Japan: Ryukyu Islands	Y	1		Early 1990s	Katsuren et al., 1996; Akamine & Nishimura, 1998; Ota, 1995, 1999	
	US: Florida	N	1	Religious	Early 1970s	L.D. Wilson & Porras, 1983	

<i>Naja najaja</i>	US: Florida	N	1	Pet trade	1970s	L.D. Wilson & Porras, 1983	Alcover et al., 1984; Griffiths et al., 1998; Schley & Griffiths, 1998; R.D. Moore et al., 2004a, b
<i>Natrix maura</i>	Balearic Islands	Y	1	Cargo stowaway	~0 A.D.	Alcover & Mayol, 1981; Kotsakis, 1981; Tonge, 1986; J. Rivera & Arribas, 1993; Corbett, 1989; Esteban et al., 1994; Pleguezuelos, 2004; Mayol, 2003; Guicking et al., 2006	
	Belgium	N	1			Parent, 1983	
	Canary Islands	N	1	Pet trade		Rodríguez Luengo, 2001; Pleguezuelos, 2004	
	France	N	1	Pet trade		Parent, 1981	
	France: Corsica	Y	2		1980, 1985	Fons et al., 1991; Lanza et al., 1992; Hafner, 1997; Naulleau & Schätti, 1997	
	Great Britain	N	1	[Cargo stowaway, pet trade]	1953	Edwards, 1953; Fitter, 1959; J.F.D. Frazer, 1964; Yalden, 1965	
(syn: <i>Natrix viperina</i>)	US: Pennsylvania	N	1	Cargo stowaway	1943	Dillon, 1944	
<i>Natrix natrix</i>	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	
	Great Britain	N	3	Intentional (3)		Fitter, 1959; Arnold & Ovenden, 2002	
	Ireland	N	5	Intentional (5)	1831, 1840, 1928	Fitter, 1959	
	Italy: Vulcano	N	1	Cargo stowaway	1955	Bruno, 1970; Lanza, 1973; Corti et al., 1997; Lo Cascio & Navarra, 2003	
	Malta	N	1			Lanza, 1973	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Natrix tessellata</i>	Belgium	N	1			de Wavrin, 1974; Parent, 1983	
	France	N	1	Pet trade		Parent, 1981	
	Germany	N	1	Pet trade		Geiger & Niekisch, 1983	
	Great Britain	N	5	Pet trade (2)	1955, 1960s, 1971, 1973, 1976	J.F.D. Frazer, 1964; Yalden, 1965; Spellerberg, 1975; C. Lever, 1977, 1980; M.J.A. Thompson, 1979; D. Frazer, 1989; Beebee & Griffiths, 2000	
	Switzerland	Y	5		1920s, 1944, 1950, 1960	Stemmler, 1967; Hotz & Broggi, 1982; Kramer & Stemmler, 1986, 1988; Geiger & Waitzmann, 1996; Gruschwitz et al., 1999	
	US: Virginia	N	1	Cargo stowaway	1982	Mitchell, 1994	
<i>Nerodia erythrogaster</i>	US: Virginia	N	2	Pet trade (2)	1939, 1974	Linzey & Clifford, 1981	
<i>Nerodia fasciata</i> (syn: <i>Natrix fasciata</i>)	US: California	Y	3	Pet trade	Early 1990s	Bury & Luckenbach, 1976; P.R. Brown, 1997; Balfour & Stitt, 2002; Stitt & Balfour, 2003; Jennings, 2004; Fuller & Trevett, 2006; Balfour et al., 2007a	
(syn: <i>Natrix fasciata</i>)	US: Texas	Y	1	Pet trade	<1957	Conant, 1977	

<i>Nerodia rhombifer</i>	US: Hawaii	N	1		1990s	Kraus & Cravalho, 2001
<i>Nerodia sipedon</i>	US: California	N	2	Pet trade	1974	Jennings, 1987a, 2004; P.R. Brown, 1997; Fuller & Trevett, 2006; Balfour et al., 2007b
<i>Nerodia taxispilota</i>	US: Colorado	N	1	Pet trade	Mid-1980s	Livo et al., 1998
<i>Ninia sebae</i>	US: Hawaii	N	1	Cargo stowaway	2000	Kraus & Cravalho, 2001
<i>Notechis scutatus</i>	Australia	Y	1	Exhibit	§1929	Bonnet et al., 1999
<i>Notechis sp.</i>	New Zealand	N	1	Cargo stowaway		Gill et al., 2001
<i>Ophedryx aestivus</i>	US: California	N	1	Pet trade		Jennings, 1987a, 2004; P.R. Brown, 1997
<i>Oxybelis sp.</i>	US: Florida	N	1	Pet trade	1960s	Bartlett, 1967a
<i>Oxyuramus scutellatus</i>	Australia	N	1	Cargo stowaway	1990s	O'Dwyer et al., 2000
<i>Pelamias platurus</i>	Colombia	?	3		1978, 1979, 1985	Rueda-Almonacid, 1999
<i>Philodryas psammophideus</i>	Brazil	N	2	Pet trade (2)	1990s (2)	Eterovic & Duarte, 2002
<i>Philodryas sp.</i>	Brazil	N	1	Pet trade	1990s	Eterovic & Duarte, 2002
<i>Pituophis catenifer</i>	US: Hawaii	N	4	Cargo stowaway (2), pet trade (1)	1990s (3)	Hunsaker & Breesse, 1967; Kraus & Cravalho, 2001
<i>Pituophis melanoleucus</i>	US: Illinois	N	1	Pet trade	1996	Anton, 1999
	US: Massachusetts	N	1	Intentional	1960s	Lazell, 1976; Cardoza et al., 1993
<i>Platycephalus florulentus</i> (syn. <i>Coluber florulentus</i>)	Egypt	N	1	Cargo stowaway	1999	Ibrahim, 2001a; Baha el Din, 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Protobothrops elegans</i> (syn: <i>Trimeresurus elegans</i>)	Japan; Ryukyu Islands	Y	1	Exhibit	1976	Ota, 1995, 1999, 2000; Katsuren et al., 1996; Akamine & Nishimura, 1998; Nishimura & Akamine, 2002; Goris & Maeda, 2004; Ota et al., 2004a; Toda & Yoshida, 2005	H. Hasegawa, 1985; Nakachi, 1993; Ota, 2002d
<i>Protobothrops flavoviridis</i> ? (syn: <i>Trimeresurus flavoviridis</i>)	Guam	N	1	Cargo stowaway	1986	Fritts, 1987	
<i>Protobothrops mucrosquamatus</i> (syn: <i>Trimeresurus mucrosquamatus</i>)	Japan; Ryukyu Islands	Y	1			Katsuren et al., 1996; Nishimura et al., 1996; Akamine & Nishimura, 1998; Itô et al., 2000; Ota, 2000; Ota et al., 2004a; Toda & Yoshida, 2005	Nishimura, & Akamine, 2000; Nishimura, 2001, 2005, 2007; Terada, 2003
<i>Pseudechis porphyriacus</i>	New Zealand	N	1	Intentional		Robb, 1986	
<i>Pseudonaja textilis</i>	Australia	N	1	Cargo stowaway	1993–1994	Limpus et al., 1999	
	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Python curtus</i>	St. Maarten	N	1	Pet trade		Powell et al., 2005	
<i>Python molurus</i>	Brazil	N	4	Pet trade (4)	1990s (4)	Eterovic & Duarte, 2002	
	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	
	US: California	N	4	Pet trade (4)	1984	Bury & Luckenbach, 1976; Jennings, 1987a, 2004	

US: Florida	Y	14	Pet trade (14)	1980s, 1990, 1990s (2)	Klimkenberg, 1993; Dalrymple, 1994; Meshaka et al., 2000, 2004a; Franke & Telecky, 2001; Bartlett & Bartlett, 2005; D.U. Greene et al., 2007	Brien et al., 2007; Snow et al., 2007a, b
US: Hawaii	N	2	Cargo stowaway, pet trade	1976, 1990s	Fritts, 1987; Kraus & Cravalho, 2001	
US: Illinois	N	1	Pet trade	1997	Anton, 1999	
US: Iowa	N	1	Pet trade	1999	Christiansen, 2001	
US: Massachusetts	N	4	Pet trade (4)		Cardoza et al., 1993	
Brazil	N	8	Pet trade (8)	1990s (8)	Eterovic & Duarte, 2002	
Canary Islands	N	2	Pet trade (2)		Pleguezuelos, 2004	
Germany	N	1	Pet trade		Geiger & Waitzmann, 1996	
St. Maarten	N	1	Pet trade		Powell et al., 2005	
US: Colorado	N	1	Pet trade	~1979	Livo et al., 1998	
US: Florida	N	13	Pet trade (13)		Meshaka et al., 2000; Bartlett & Bartlett, 2005	
US: Hawaii	N	1	Pet trade	1990s	Kraus & Cravalho, 2001	
Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	
Germany	N	3	Pet trade (3)	1980s (3)	Münch, 1992	
US: California	N	3	Pet trade (3)		Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
US: Colorado	N	1	Pet trade	~1984	Livo et al., 1998	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Florida	?	1	Pet trade		Klimkenberg, 1993; Dalrymple, 1994; Meshaka et al., 2000, 2004a; Franke & Telecky, 2001	
	US: Hawaii	N	1	Pet trade	1990s	Kraus & Cravalho, 2001	
	US: Massachusetts	N	4	Pet trade (4)	1980s (1)	Cardoza et al., 1993	
<i>Python sebae</i>	Brazil	N	2	Pet trade (2)	1990s (2)	Eterovic & Duarte, 2002	
	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	
	Germany	N	2	Pet trade (2)	1980s (2)	Münch, 1992	
	US: Florida	?	1			Dalrymple, 1994; Meshaka et al., 2004a	
<i>Python</i> sp.	Brazil	N	3	Pet trade (3)	1990s (3)	Eterovic & Duarte, 2002	
	US: Colorado	N	1	Pet trade	1993	Livo et al., 1998	
<i>Ramphotyphlops braminus</i>	American Samoa	Y	1	Nursery trade	1990s	Craig, 2002; Goldin, 2002	
	Anguilla	Y	1	Nursery trade	1996	Censky & Hodge, 1997; Hodge et al., 2003	
	Argentina	Y	1			Loveridge, 1957	
	Aruba	Y	1	Nursery trade	2003	van Buurt, 2006	

Australia	Y	1	Nursery trade	Early 1960s	Storr, 1968; Cogger et al., 1983b; Covacevich & Couper, 1991; Cogger, 1992; Ehmann, 1992; Coate, 1997; Richards & Calvert, 1999; Maryan, 2001; Gaikhorst, 2005; Andersen et al., 2005; S. Wilson, 2005
Bahrain	Y	1			Gallagher, 1971; David & Vogel, 1996
Benin	Y	1			David & Vogel, 1996
Cameroon	Y	1			Roux-Estève, 1974
Canary Islands	Y	1			López-Jurado et al., 2006
Cayman Islands	Y	1	Nursery trade		Hodge et al., 2003; Echternacht & Burton, 2003
Central African Republic	Y	1			Chirio & Ineich, 1997
Christmas Island	Y	1		1930s	Cogger et al., 1950; Gibson-Hill, 1950; Cogger, 1992
Cocos-Keeling Island	Y	1			Wood Jones, 1909; Cogger et al., 1950; Gibson-Hill, 1950; Cogger, 1992
Comoros	Y	1	Nursery trade		Loveridge, 1957; Guibé, 1958; Meirte, 1999a, 2004

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Egypt	Y	1	Nursery trade	1984	Baha el Din, 1996, 2001, 2006; Saleh, 1997; Wallach, 1999; Ibrahim, 2005	
	El Salvador	Y	1	Nursery trade		Köhler et al., 2006	
	Equatorial Guinea	Y	1			Jesus et al., 2003	
	Fiji	Y	1			C. Morrison, 2003	
	FSM	Y	1			McDowell, 1974; L.A. Thomas, 1997; Buden, 2000a	
	Gabon	Y	1			Pauwels et al., 2004	
	Guatemala	Y	1			Dixon & Hendricks, 1979	
	Iran	Y	1			McDowell, 1974	
	Iraq	Y	1			David & Vogel, 1996	
	Ivory Coast	Y	1			Roux-Estève, 1974	
	Japan: Izu Islands	Y	1	Nursery trade		Ota et al., 1995b, Kazuki, 2001; Uchiyama et al., 2002	
	Japan: mainland	Y	2	Nursery trade (2)	<1917, >1960	Hikida et al., 1992; Ota et al., 1995; M. Hasegawa, 1999; Ota, 2000; Kazuki, 2001; Toda & Yoshida, 2005	
	Japan: Ogasawara Islands	Y	1			Hara, 1986; Kazuki, 2001; Uchiyama et al., 2002; Toda & Yoshida, 2005	

Japan: Ryukyu Islands	Y	1	Takara, 1962; Ota, 1986a; Ota et al., 1993; Kamosawa & Ota, 1996 Ota et al., 1991, 2004; Toyama & Ota, 1991; Hiksida et al., 1992; Kazuki, 2001; Uchiyama et al., 2002; Toda et al., 2003
Kenya	Y	1	Loveridge, 1957; Broadley & Howell, 1991
Kiribati	Y	1	David & Vogel, 1996
Kuwait	Y	1	David & Vogel, 1996
Loyalty Islands	Y	1	Bauer & Vindum, 1990; Shea & Wallach, 2000
Madagascar	Y	1	Loveridge, 1957; Guibé, 1958; Raselimana & Vences, 2003
Marshall Islands	Y	1	J.L. Knight, 1984; Lamberson, 1987; Spennemann, 1997
Mauritania	Y	1	Trape & Ba, 2006
Mauritius	Y	1	Daruty de Grandpré, 1883; Koenig, 1932; Guibé, 1958; J. Vinson, 1964; Blanc, 1972; Cheke, 1987; Tonge, 1990

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Mexico	Y	1		<1900	Shreve, 1938; E.H. Taylor, 1940; H.M. Smith & Taylor, 1945; J.A. Peters, 1954; Loveridge, 1957; Duellman, 1961; Hardy & McDiarmid, 1969; McDowell, 1974; H.M. Smith and Smith, 1976; Dixon & Hendricks, 1979; R.W. Murphy & Ottley, 1979; Dundee & Flores-Villela, 1991; Mendoza Quijano et al., 1993, 1994, 2001; Castro-Franco & Bustos Zagal, 1994; Ellosa-Leon et al., 1995; Alvarez & Murillo, 1996; Mancilla-Moreno & Ramirez-Bautista, 1998; Guzmán & Muñiz-Martínez, 1999; Nevárez, 1999; de la Torre-Loranca et al., 2000; Vázquez-Díaz & Quintero-Díaz, 2001; Valdespino & García-M., 2000; Cedefio-Vázquez et al., 2003; Ponce-Campos et al., 2003; Solano Zavaleta et al., 2006; Mata-Silva & Ramirez-Bautista, 2007; Quijada-Mascareñas & Canseco-Márquez, 2007b; Quijada-Mascareñas & Enderson, 2007	

Mozambique	Y	I			Loveridge, 1957; Roux-Estève, 1974; Broadley & Howell, 1991; Marais, 1992
New Caledonia	Y	I	<1974		Bauer, 1987, 1999; Bauer & Vindum, 1990; Ineich & Bauer, 1992; Gargominy et al., 1996; Bauer & Sadlier, 2000
New Zealand	N	I			Gill et al., 2001
Nigeria	Y	I			David & Vogel, 1996
Oman	Y	I			David & Vogel, 1996; van der Kooij, 2001a, b
Pakistan	Y	I			Minton, 1966
Palau	Y	I			McDowell, 1974; Crombie & Pregill, 1999
Papua New Guinea	Y	I			McDowell, 1974; O'Shea, 1996
Réunion	Y	I	<1862	Nursery trade	Maillard, 1862; A. Vinson, 1868; Mertens, 1934; Bour & Moutou, 1982; Cheke, 1987
Rodrigues	Y	I			J. Vinson, 1964; Blanc, 1972; Bour & Moutou, 1982; Cheke, 1987
Saudi Arabia	Y	I			Loveridge, 1957; David & Vogel, 1996
Senegal	Y	I	1980s		Trape, 1990
Seychelles	Y	I	1930s		Vesey-FitzGerald, 1947; Honegger, 1966; Gaymer, 1968; Nussbaum, 1980, 1984; Matyot, 2001
					Wynn et al., 1987; Matyot, 2003

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Solomon Islands	Y	1			Loveridge, 1957; M. McCoy, 1980	
	Somalia	Y	1			Gans & Laurent, 1965; Roux-Estève, 1974; Broadley & Howell, 1991	
	South Africa	Y	1		1840s	FitzSimons, 1936; Loveridge, 1957; McLachlan, 1978; Visser, 1979; Broadley, 1983; Brooke et al., 1986; Marais, 1992; Bourquin, 2004	
	St. Barts	Y	1	Nursery trade	1990s	Breuil, 2002; Hodge et al., 2003	
	St. Maarten	Y	1	Nursery trade	1990s	Breuil, 2002; Hodge et al., 2004; Powell et al., 2005	
	Taiwan	Y	1			Horikawa, 1930; McDowell, 1974; Lue et al., 1992, 2003	Ota et al., 1993
	Tanzania	Y	1		<1939	Loveridge, 1955, 1957; Roux-Estève, 1974; Pakenham, 1983; Broadley & Howell, 1991	
	Tanzania: Pemba Island	Y	1			David & Vogel, 1996	
	Tanzania: Zanzibar	Y	1			Loveridge, 1957; Roux-Estève, 1974	
	Togo	Y	1			David & Vogel, 1996	

United Arab Emirates	Y	1	David & Vogel, 1996
US: Alabama	Y	3	Bartlett & Bartlett, 2005
US: Arizona	N	1	Rosen & Schwalbe, 2002
US: Florida	Y	1	L.D. Wilson & Porras, 1983; Delorey & Mushinsky, 1987; Lazell, 1989a; Ehrig, 1990; Crawford & Somma, 1993a; Meshaka, 1994b; Watkins-Colwell & Watkins-Colwell, 1995c; Butterfield et al., 1997; R.D. Owen et al., 1998; Ernst & Brown, 2000; Krysko et al., 2000; Meshaka et al., 2000, 2004a; J.T. Collins & Collins, 2002; Townsend et al., 2002; Grace & Van Dyke, 2004; Hennessy & Michalak, 2004; Bartlett & Bartlett, 2005; Krysko et al., 2005; Klowden & Olson, 2007; Somma, 2007; Somma & Skelley, 2007
(syn: <i>Typhlops braminus</i> , <i>Typhlina braminica</i>)	Y	2	Wynn et al., 1987; Enge et al., 2004b Bartlett & Bartlett, 2005; Jensen, 2007

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Hawaii	Y	1	Nursery trade	1920s	Slevin, 1930; Mertens, 1934; Tinker, 1938; Fisher, 1948; Oliver & Shaw, 1953; Hunsaker & Breese, 1967; Lieberman & Lieberman, 1970; McKeown, 1996	Wynn et al., 1987
	US: Louisiana	Y	1	Nursery trade	1993	R.A. Thomas, 1994	
	US: Massachusetts	Y	1	Nursery trade	1990	Wallach et al., 1991; Cardoza et al., 1993; G.S. Jones et al., 1995	
	US: Texas	Y	2			Dixon, 2000; Bartlett & Bartlett, 2005; Godwin et al., 2007	
	US: Virginia	Y	1		2000	Savitzy et al., 2002	
	Vanuatu	Y	1	Cargo stowaway	1971	Medway & Marshall, 1975; Anonymous, 1981; Shea & Wallach, 2000	
	Yemen: Socotra	Y	1			Loweridge, 1957	
<i>Rhinoplocephalus nigrescens</i>	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Simoselaps bimaculatus</i>	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Sistrurus miliaris</i>	US: Virginia	N	1	Pet trade	1957	Mitchell, 1994	
<i>Spalerosophis diadema</i>	US: Hawaii	N	1	Cargo stowaway	1986	Fritts, 1987	
<i>Spilotes pullatus</i>	US: Florida	N	1	Pet trade	1960s	Bartlett, 1967a	
	US: Indiana	N	1	Cargo stowaway		Minton, 1972	

<i>Storeria dekayi</i>	Bahamas	Y	1	Nursery trade	1990s	D.S. Lee, 2004, 2005	Gittenberger & Hoogmoed, 1985
<i>Suta ordensis</i>	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
<i>Tantilla melanocephala</i>	Mustique	N	1	Cargo stowaway	2005	Henderson & Powell, 2006	
<i>Telescopus fallax</i>	Greece: islands	Y	1	Religious		Warnecke, 1988	
(syn: <i>Tarbophis fallax</i> , <i>Tarbophis vivax</i>)	Malta	Y	1	Cargo stowaway	1910s	Giglioli, 1896; Despoit, 1915; Mertens, 1921, 1924, 1968; Borg, 1939; Lanfranco, 1955; Schembri, 1984; Savonia-Ventura, 1985; Lanza, 1987; Lanza & Corti, 1993, 1996	
<i>Thamnophis brachystoma</i>	US: New York	Y	2			Wright & Wright, 1957; Bothner, 1976; Conant & Collins, 1998	
	US: Ohio	Y	1		1980s	Novotny, 1990	
	US: Pennsylvania	Y	3			Conant, 1975; Bothner, 1976; Lethaby, 2004	
<i>Thamnophis cyrtopsis</i>	Curaçao	N	1	Nursery trade		van Buurt, 2005	
<i>Thamnophis elegans</i>	Germany	?	20	Pet trade (20)	1980s (20)	Münc, 1992	
	US: Hawaii	N	1	Pet trade		Hunsaker & Breese, 1967	
<i>Thamnophis radix</i>	US: Colorado	N	1	Pet trade	1957	Livo et al., 1998	
<i>Thamnophis sauritus</i>	Bahamas	N	1	Nursery trade	1997	Buckner & Franz, 1998a; D.S. Lee, 2004, 2005	
	US: California	N	1	Exhibit	1935	Jennings, 1987a, 2004; P.R. Brown, 1997	
<i>Thamnophis sirtalis</i>	Austria	?	1	Intentional	1973	Sochurek, 1978	
	Bahamas	N	1	Cargo stowaway	1997	Buckner & Franz, 1998b; D.S. Lee, 2004, 2005	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Brazil	N	1	Pet trade	1990s	Eterovic & Duarte, 2002	
	Germany	?	20	Pet trade (20)	1980s (20)	Münch, 1992	
	Great Britain	N	3	Intentional (1), pet trade (2)	1967	Beebee & Griffiths, 2000	
	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
	Sweden	N	1	Pet trade	1980s	Ahlén et al., 1995	
	Guam	N	1	Cargo stowaway	1996	Wiles, 2000	
<i>Thamnophis</i> sp.	Netherlands	N	2		1985, 1987	Melchers & Timmermans, 1991	
	US: Hawaii	N	3	Cargo stowaway (2), pet trade	1990s (3)	Kraus & Cravalho, 2001	
	US: New Jersey	N	1	Intentional	§1964	Rothman, 1965	
<i>Trimeresurus popeiorum</i>	New Zealand	N	1	Cargo stowaway		Gill et al., 2001	
typhlopid sp.	FSM	?	1		1999	Buden et al., 2001	
<i>Typhlops lumbricalis</i> (syn: <i>Typhlops tumbricalis</i>)	US: Florida	N	1		1930	C.W. Myers, 1958; Ashton, 1967; L.D. Wilson & Porras, 1983	
<i>Typhlops porrectus</i>	Mascarene Islands	Y	1			C. Lever, 2003	
<i>Typhlops pusillus</i>	US: Florida	?	1			Schwartz & Henderson, 1988, 1991	
<i>Vipera ammodytes</i>	Austria	?	1			Cabela & Tiedemann, 1985	
	Germany	N	1	Pet trade		Geiger & Waitzmann, 1996	
	Switzerland	Y	1			Crnobrnja-Ikaitovic & Haxhiu, 1997	

<i>Vipera aspis</i>	Belgium	N	1			Parent, 1983
	France	Y	7	Intentional (1), research (6)	1973 (3), 1979 (2), 1987	Pascal et al., 2006
	Italy	Y	1			Bruno, 1985; Corti et al., 1997, 2006; Lo Cascio & Navarra, 2003
<i>Vipera berus</i>	Germany	N	5	Nursery trade, pet trade (2)	1881, 1960, 1986, 1988	Geiger & Nickisch, 1983; Bammerlin & Bitz, 1996
	Japan: Ryukyu Islands	N	1		1994	Katsuren et al., 1996
<i>Xenochrophis piscator</i>	Singapore	Y	1			Lim & Chou, 1990; Lim & Lim, 1992
<i>Zamenis longissimus</i> (syn: <i>Elaphe longis-</i> <i>sima</i>)	Germany	N	11	Intentional (3), medicine (1), pet trade (6)	1853, 1854, 1905, 1947, 1960s (2), late 1970s, 1980s, 1990, 1993 (2)	Jaeschke, 1971; Münch, 1992; Böhme, 1993; Heimes & Waitzmann, 1993; Bammerlin & Bitz, 1996; Geiger & Waitzmann, 1996
	Great Britain	Y	1	Zoo trade	1960s	Beebee & Griffiths, 2000; Arnold & Ovenden, 2002
TURTLES	Switzerland	Y	3			Hofer, 2001
	Canada: Vancouver Island	N	3		1933, 1936, 1959	F.R. Cook, 1984; Stebbins, 1985
<i>Actinemys marmorata</i>	US: Oregon	Y	1			Stebbins, 1985

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Aldabrachelys gigantea</i> (syn: <i>Dipsochelys dussumieri</i> , <i>Dipsochelys hololissa</i>)	Chagos Archipelago	N	1		1771	Gerlach & Canning, 1998	
(syn: <i>Dipsochelys dussumieri</i> , <i>Geochelone gigantea</i> , <i>Testudo gigantea</i>)	Mauritius	Y	3	Food (2)	§1820, 1883	Bour, 1984a, b; Cheke, 1987; Tonge, 1990	
(syn: <i>Dipsochelys dussumieri</i> , <i>Geochelone gigantea</i> , <i>Testudo gigantea</i>)	Réunion	?	1	Food	Early 1800s	A. Vinson, 1868; Bour & Moutou, 1982	
(syn: <i>Dipsochelys dussumieri</i> , <i>Geochelone gigantea</i> , <i>Testudo gigantea</i>)	Seychelles	Y	21	Conservation (2), exhibit (3)	1883, 1896, 1978, 1980, 1982	A. Günther, 1898; Davidson, 1911; Stoddart & Poore, 1970; Feare, 1979; Stoddart & Fosberg, 1981; Stoddart et al., 1982; Bour, 1984c; Samour et al., 1987; Hamblen, 1994; Gerlach & Canning, 1998; Karanth et al., 2005	Austin et al., 2003; Palkovacs et al., 2003
(syn: <i>Dipsochelys dussumieri</i> , <i>Geochelone gigantea</i> , <i>Testudo gigantea</i>)	Tanzania	Y	1		Early 1800s	Gerlach & Canning, 1998	
<i>Amyda cartilaginea</i>	Hong Kong	N	1			Karsen et al., 1998	
<i>Apalone ferox</i> (syn: <i>Trioryx ferox</i>)	US; Florida	Y	1			Iverson & Eichberger, 1989; Lazell, 1989a	

(syn: <i>Trionyx ferox</i>)	US: North Carolina	N	1	Pet trade	1900	Brimley, 1944; Palmer & Braswell, 1995
<i>Apalone spinifera</i>	France	N	1	Pet trade		Haffner, 1997
(syn: <i>Trionyx emoryi</i> , <i>Trionyx spinifera</i>)	Mexico	Y	2	Spread from adjacent introduction	[1928]	Cowles & Bogert, 1936; Linsdale & Gressitt, 1937; Miller, 1946; McPeak, 2000; Grismer, 2002a; Castro-Franco & Bustos Zagal, 2004
(syn: <i>Trionyx emoryi</i> , <i>Trionyx spinifera</i>)	US: Arizona	Y	1	Food	§1900	K.P. Schmidt, 1924; Cowles & Bogert, 1936; Linsdale & Gressitt, 1937; Dill, 1944; Hardy & Lamoreaux, 1945; Miller, 1946; Webb, 1962; Hahn & May, 1972; McCoid, 1995a; Brennan & Holycross, 2005
(syn: <i>Trionyx emoryi</i> , <i>Trionyx spinifera</i>)	US: California	Y	2	Spread from adjacent introduction, pet trade	[1929], 1990s	Storer, 1933a; Cowles & Bogert, 1936; Linsdale & Gressitt, 1937; Dill, 1944; Miller, 1946; Webb, 1962; Bury & Luckenbach, 1976; Vitt & Ohmart, 1978; Jennings, 1987a, 2004; McCoid, 1995a; Spinks et al., 2003
	US: Hawaii	Y	1	Intentional	1990s	Yamamoto & Tagawa, 2000
	US: Illinois	N	1			Lamer et al., 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Maryland	?	4	Food, intentional, pet trade	1883, 1950s, 1991, 2003	Dukehart, 1884; Mansueti & Wallace, 1960; Cooper, 1961; Harris, 1975, 2004; Rambo, 1992	
	US: Massachusetts	N	1		1988	Cardoza et al., 1993	
	US: Nevada	Y	1	Spread from adjacent introduction	[1935]	Cowles & Bogert, 1936; Linsdale & Gressitt, 1937; Linsdale, 1940; Miller, 1946; Webb, 1962	
(syn: <i>Trionyx spinifer</i>)	US: New Jersey	Y	1	Intentional	1910	Conant, 1961; Webb, 1973; Ernst et al., 1994; Hulse et al., 2001	
	US: New Mexico	Y	1		~1900	Dill, 1944; Miller, 1946	
	US: Pennsylvania	?	1			Hulse et al., 2001	
	US: Utah	Y	1	Spread from adjacent introduction	[1976]	Roby & Loveless, 1977	
(syn: <i>Trionyx spiniferus</i>)	US: Virginia	N	1	Pet trade		Ernst et al., 1997	
<i>Apalone</i> sp.	Japan: mainland	N	1	Pet trade		Yasukawa, 2005	
chelid sp.	Palau	?	1		1937	Aoki, 1977; Crombie & Pregill, 1999	
<i>Chelodina expansa</i>	Australia	?	1	Pet trade		Larwill, 1995; Low, 2003	
<i>Chelodina longicollis</i>	Australia: Tasmania	Y	1	Pet trade		Roberts, 1964; Rounsevell & Swain, 1993; Low, 2003	

<i>Chelus fimbriatus</i>	New Zealand	N	1			McCann, 1966; West, 1979
	US: Florida	N	1	Pet trade	1960s	W. King & Krakauer, 1966; Bartlett, 1967b
<i>Chelydra serpentina</i>	Austria	N	1			Kaltenegger, 2006
	Canada: British Columbia	N	1	Intentional	1913	Carl & Guiguet, 1972; Gregory & Campbell, 1984
	Canary Islands	N	1	Pet trade	2002	Pleguezuelos, 2004
	France	N	1	Pet trade		Haffner, 1997
	Germany	N	2	Pet trade (1)	2000s	Geiger & Niekisch, 1983; Geiger & Waitzmann, 1996; Kaltenegger, 2006
	Great Britain	N	4	Intentional (2), pet trade (2)	1905 (1)	Swanton, 1928; R.H.R. Taylor, 1948, 1963; Fitter, 1959; J.F.D. Frazer, 1964; Beebee & Griffiths, 2000; Bringsøe, 2001a; Arnold & Ovenden, 2002
	Guam	?	3	Pet trade (3)	1997, 1998 (2)	Leberer, 2003
Italy	N	2	Pet trade	1987	Ferri, 1996; Bagnoli & Carpaneto, 2000	
Japan: mainland	Y	3	Pet trade		Uchiyama et al., 2002; Ota, Ishida et al., 2004; Kobayashi et al., 2006a	
US: Arizona	Y	1			2005; Toda & Yoshida, 2005; Yasukawa, 2005; M. Sato & Suzuki, 2006	
						Hulse, 1980; McCoid, 1995a; Brennan & Holycross, 2005

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: California	Y	14	Pet trade (14)	1972, 1990s	Stebbins, 1972; Bury & Luckenbach, 1976; Jennings, 1987a, 2004; Holland, 1994; Spinks et al., 2003	
	US: Colorado	N	1	Pet trade	1970	Livo et al., 1998	
	US: Nevada	Y	1			Stebbins, 1985; F.W. King & Burke, 1989	
	US: New Mexico	?	1		1990s	Stuart & Painter, 1988; Stuart & Clark, 1991; Stuart, 1995b; Degenhardt et al., 1996	
	US: Oregon	?	5			Storm & Leonard, 1995	
	US: Utah	Y	1			Stebbins, 1985; F.W. King & Burke, 1989	
	US: Washington	?	3			K.R. McAllister, 1995; Storm & Leonard, 1995; Hays et al., 1999	
<i>Chersina angulata</i>	Namibia	Y	2	Pet trade (2)		M. Griffin, 2000	
<i>Chrysemys picta</i>	Austria	N	2			Kallenegger, 2006	
	Germany	?	3			Podloucky, 1998; M. Fritz & Lehmann, 2002	
	Great Britain	N	4	Intentional (2), pet trade (2)	1905 (1)	Swanton, 1928; R.H.R. Taylor, 1948, 1963; Fitter, 1959; J.F.D. Frazer, 1964; Beebee & Griffiths, 2000; Arnold & Ovenden, 2002	

	Malta	N	1	Intentional	1910s	Despott, 1913
(syn: <i>Psuedemys picta</i>)	Spain	Y	4	Pet trade (4)		Mateo, 1997a; Barbadillo et al., 1999; Pleguezuelos, 2004
	US: Arizona	N	5	Pet trade (5)	1960s, 2002	Hulse, 1980; Jennings, 1987d; Boundy, 1991; Lazaroff et al., 2006
	US: California	?	7	Intentional (1), pet trade (5)	1974, 1990s	Banta & Morafka, 1966; Bury & Luckenbach, 1976; Stebbins, 1985; Jennings, 1987a, 2004; Holland, 1994; Spinks et al., 2003
	US: Colorado	?	3	Pet trade (3)	1947, 1993	Rodeck, 1948; Livo et al., 1998
	US: Florida	N	3	Pet trade (3)	1938, 1964, 1983	W. King & Krakauer, 1966; Bartlett, 1967b; Iverson & Eichberger, 1989; F.W. King & Burke, 1989
	US: Illinois	N	1	Pet trade	1971	Dancik, 1974
	US: New Mexico	?	2		1998, 2000	Stuart, 2000, 2001
<i>Clemmys guttata</i>	US: Illinois	?	2	Pet trade	1972	Dancik, 1974
<i>Cuora amboinicus</i>	US: Illinois	N	1	Pet trade	1990s	Anton, 1999
<i>Cuora flavomarginata</i>	Hong Kong	N	3	Pet trade (3)	1980 (2), 1984	Karsen et al., 1998
(syn: <i>Cuora evelynae/flavomarginata</i>)	Japan: Ryukyu Islands	Y	10	Pet trade (10)	1980s (2), 1996, 1999, 2001 (2), 2003	Ota, 1995, 1999; Masuno et al., 1998; Goris & Maeda, 2004; Oka, 2004; Ota et al., 2004a; Shiroma & Ota, 2004; Toda & Yoshida, 2005

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Illinois	N	1	Pet trade	1990s	Anton, 1999	
	US: Massachusetts	N	2		1990, 1992	Cardoza et al., 1993	
<i>Cuora trifasciata</i>	Namibia	N	1	Pet trade		M. Griffin, 2000	
	US: Hawaii	N	1	Food	1920s	Lovich, 1989	
<i>Cuora</i> sp.	US: Illinois	N	1			Anton, 1999	
<i>Deirochelys reticularia</i>	US: Florida	?	1	Pet trade	1989	Butterfield et al., 1994b	
<i>Eelseya dentata</i>	Australia	?	1	Pet trade		Low, 2003	
<i>Eelseya latisternum</i>	Australia	Y	1	Pet trade		Low, 2003; Swan et al., 2004	
<i>Elasor macrurus</i>	Australia	?	1	Pet trade		Low, 2003	
emydid sp.	Guam	N	1	Pet trade	1991	McCoid, 1993a	
<i>Emydoidea blandingi</i>	US: Connecticut	N	1			DeGraaf & Rudis, 1983	
	US: Kansas	N	1	Pet trade	1979	Collins, 1993	
	US: Maryland	N	2	Pet trade (2)	1938, 1969	Mansueti, 1941a; McCauley, 1945; Carver, 1970	
<i>Emydura macquarii</i>	Australia	Y	4	Pet trade (2)		D. Green, 1994; Larwill, 1995; Low, 2003; Swan et al., 2004	
<i>Emydura signata</i>	Australia	Y	1			K. Griffiths, 1997; Low, 2003	
<i>Emydura</i> sp.	Australia	Y	1	Intentional	1946	A.J. Bartlett, 1948; Copley, 1994	

<i>Emys orbicularis</i>	Austria	Y	36	Intentional (11)	1824, 1920, 1962, 1980s (8), 1990	Eiselt, 1961; Sochurek, 1978, 1985; Street, 1979; Cabela, 1985; Cabela & Tiedemann, 1985; Lutschinger, 1989; Grillitsch, 1990; Podloucky, 1997; Gemel, 2001; U. Fritz, 2001; Kaltenecker, 2006
	Balearic Islands	Y	2	Pet trade		K. Lehmann, 1980; Alcover & Mayol, 1981; Dutton, 1981a; Vickers, 1983; J. Rivera & Arribas, 1993; Esteban et al., 1994; Kramer, 1995; U. Fritz et al., 1998; U. Fritz, 2001, 2003; Salvador & Pleguezuelos, 2002; Pleguezuelos, 2004
	Belgium	N	25	Intentional (2)	1880s (2)	de Wavrin, 1974; Parent, 1981, 1983; Gubbels, 1992; U. Fritz, 2001, 2003
	Czech Republic	N	13	Intentional, pet trade	1603, 1687, 1901	Podloucky, 1997; Moravec, 1999; Široký, 2000; U. Fritz, 2001, 2003;
	Denmark	?	6	Pet trade (4)	1950s, 1990s (3)	J. Christiansen, 1974; Bringsøe & Graff, 1994; Bringsøe, 1997, 2001b, 2002; Podloucky, 1997; U. Fritz, 2001, 2003; Balle, 2002; Jensen, 2002; Kjærgaard, 2002

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	France	Y	15			Street, 1979; Parent, 1981; Frey, 1986; Colin, 1992; U. Fritz, 2001, 2003	
	Germany	Y	191	Food (2), intentional (2), pet trade (13)	1669, 1880, 1910, 1940s, 1980 (2), 1981, 1988	Friedel, 1868; Emmel, 1936; Rühmekorf, 1970/1971; Latzel, 1977; Preywisch & Steinborn, 1977; Gersner et al., 1978; Street, 1979; Parent, 1981; Geiger & Niekisch, 1983; Podloucky, 1985, 1997, 1998; Neseemann, 1986, 1987; Eckstein & Meinig, 1989; Kordges et al., 1989; U. Fritz & Günther, 1996; Buddle, 1998; Hanka & Jøger, 1998; U. Fritz, 2001, 2003; U. Fritz et al., 2004	Lenk et al., 1998
	Great Britain	N	10	Intentional (5), pet trade (5)	1890, 1894, 1905, 1906 (2), 1938, 1950s, 1960s, 1970s(2)	Swanton, 1928; R.H.R. Taylor, 1948, 1963; Fitter, 1959; J.F.D. Frazer, 1964; Yalden, 1965; Buckley, 1974; C. Lever, 1977; Beebe & Griffiths, 2000; Bringsøe, 2001a; Arnold & Ovenden, 2002	
	Ireland	N	1	Intentional	1906	C. Lever, 1977	

Italy	?	2		Podloucky, 1997; Lenk et al., 1998
Luxemburg	N	11		Parent, 1981; U. Fritz, 2001, 2003
Netherlands	N	24	Pet trade (2)	Parent, 1981; Gubbels, 1992; van Wijngaarden-Bakker, 1999; U. Fritz, 2001, 2003
Poland	?	2	Pet trade (2)	Mitrus, 2000
Slovakia	Y	2		U. Fritz, 2001, 2003
Spain	Y	3	Biocontrol, intentional (2)	Pleguezuelos, 2004
Sweden	N	1		Ahlén et al., 1995
Switzerland	Y	7	Intentional (3), pet trade	Street, 1979; Hoitz & Mosimann & Cadi, 2004
<i>Geochelone carbonaria</i>	N	1	Pet trade	(4) Broggi, 1982; Kramer & Stemmler, 1986, 1988; A. Keller et al., 1993; Pillet, 1996; Dušej & Müller, 1997; Podloucky, 1997; U. Fritz, 2001, 2003
US: California	N	1	Pet trade	Bury & Luckenbach, 1976; Jennings, 1987a, 2004
US: Florida	?	1	1980s	Meshaka et al., 2004a
<i>Geochelone denticulata</i>	Y	1		Pritchard & Trebbau, 1984
US: Florida	N	1	Pet trade	Bartlett, 1967b
Malta	N	1	Intentional	Despott, 1913
<i>Geochelone elegans</i> (syn: <i>Testudo elegans</i>)				

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Geochelone pardalis</i>	US: Virginia South Africa	N Y	1 2	Pet trade	<1930, <1966	Ernst et al., 1997 Brooke et al., 1986; Branch, 1988	
<i>Geochelone radiata</i>	Mauritius	Y	2	Ballast, food	1830–1950s	Koenig, 1932; Bour, 1984a, b; Cheke, 1987; Tonge, 1990	
	Réunion	Y	2	Food	Early 1800s–1880s	Bour & Moutou, 1982	
<i>Geoemyda japonica</i>	Japan: Ryukyu Islands	?	2	Pet	1997	Ota et al., 2004a; Watanabe, 2006	
<i>Glyptemys insculpta</i> (syn: <i>Clemmys insculpta</i>)	US: Maryland	N	1	Pet trade	1939	W. Norman, 1939; McCauley, 1945; C.F. Reed, 1956; Conant, 1958; Cooper, 1960; Miller, 1993	
(syn: <i>Clemmys insculpta</i>)	US: Massachusetts	N	5	Pet trade (5)	1960 (1)	Lazell, 1976; Cardoza et al., 1993	
(syn: <i>Clemmys insculpta</i>)	US: New York	N	2	Pet trade	1960s	Burnley, 1968	
<i>Glyptemys muhlenbergii</i>	US: California	N	1		Late 1990s	Spinks et al., 2003	
<i>Glyptemys muhlenbergii</i> (syn: <i>Clemmys muhlenbergii</i>)	US: Massachusetts	N	1	Pet trade	1960	Cardoza et al., 1993	
<i>Gopherus agassizii</i>	Mexico: Baja California	?	1			Ottley & Velázquez-S., 1989; Crumly & Grismer, 1994	
	US: Colorado	N	1	Pet trade	§1966	Livo et al., 1998	
	US: New Mexico	N	5	Pet trade (1)		Degenhardt et al., 1996	

<i>Gopherus berlandieri</i>	US: Arizona	?	2	Pet trade (2)	1995	Auffenberg & Franz, 1978; Howland, 1996
	US: California	?	4	Pet trade (4)		Stebbins, 1972; Bury & Luckenbach, 1976; Jennings, 1987a, 2004
	US: Colorado	N	1	Pet trade		Livo et al., 1998
	US: Florida	N	1	Pet trade		Bartlett, 1967b
	US: Massachusetts	N	1		Late 1980s	Cardoza et al., 1993
	US: New York	N	1	Pet trade	1960s	Burnley, 1968
<i>Gopherus flavomarginatus</i>	US: Arizona	?	1			Howland, 1996
<i>Gopherus polyphemus</i>	US: Florida	N	1	Pet trade		Lazell, 1989a
	US: Massachusetts	N	2		1980s, 1991	Cardoza et al., 1993
	US: North Carolina	N	1	Pet trade		Palmer & Braswell, 1995
<i>Gopherus</i> sp.	US: Indiana	N	1			Minton, 1972
	US: Massachusetts	N	4		1980s (3), 1991	Cardoza et al., 1993
<i>Graptemys geographica</i>	US: California	N	1	Pet trade		Jennings, 1987a, 2004
	US: Massachusetts	N	1	Pet trade	1950	Moulton, 1953; Cardoza et al., 1993
	US: Pennsylvania	Y	1			Arndt & Potter, 1973; DeGraaf & Rudis, 1983; Serrao, 2000; Behler et al., 2004
<i>Graptemys ouachitensis</i>	US: Alabama	?	1		1992	Dobie et al., 1996
	US: Florida	N	1			Engel et al., 2007
<i>Graptemys pseudogeographica</i>	France	N	1	Pet trade		Haffner, 1997

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Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
(syn: <i>Graptemys kohli</i>)	Spain	N	3	Pet trade (3)		Pleguezuelos, 2004	
(syn: <i>Graptemys kohli</i>)	US: California	N	2	Pet trade		Jennings, 1987a, 2004; Holland, 1994; Spinks et al., 2003	
(syn: <i>Graptemys kohli</i>)	US: Colorado	N	1	Pet trade	1950	Livo et al., 1998	
(syn: <i>Graptemys kohli</i>)	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966; Bartlett, 1967b	
(syn: <i>Graptemys kohli</i>)	US: Illinois	N	7	Pet trade (1)	1971, 1972, 1980s (3), 1991 (1)	Dancik, 1974; Ludwig et al., 1992; Anton, 1999	
(syn: <i>Graptemys kohli</i>)	US: Iowa	N	1	Pet trade	1973	Christiansen, 2001	
(syn: <i>Graptemys kohli</i>)	US: Maryland	N	2	Pet trade	1960	Cooper, 1961; F.J. Schwartz & Dutcher, 1961	
(syn: <i>Graptemys kohli</i>)	US: Tennessee	?	1		1972	Dancik, 1974	
(syn: <i>Graptemys kohli</i>)	US: Virginia	Y	3	Pet trade (2)	1901, 1940, early 1990s	Fowler, 1943; Mitchell, 1994; Ernst et al., 1997; Savitzky & Mitchell, 2001	
<i>Graptemys</i> sp.	Japan: mainland	N	1			Yasukawa, 2005	
<i>Kinixys bellitana</i>	Madagascar	Y	1			Bour, 1978, 1987, 2006; Glaw & Vences, 1992; Pedrono et al., 2000; Pedrono & Smith, 2003; Raselimanana & Vences, 2003	
	Seychelles	N	1			Bour, 2006	

<i>Kinostemon flavescens</i>	US: New Mexico	N	2	Pet trade		Degenhardt et al., 1996; Stuart 1997
<i>Kinostemon scorpioides</i>	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966
<i>Kinostemon subrubrum</i>	US: California	N	1	Pet trade	1997	Spinks et al., 2003
	US: Connecticut	N	2	Pet trade	1960	Craig et al., 1980
	US: Massachusetts	N	2		1992 (1)	Cardoza et al., 1993
<i>Lissemys punctata</i>	Andaman Islands	Y	1			Das, 1995, 1999
	Indonesia: Sulawesi	N	1			Iskandar, 2000
	Malaysia	?	1	Religious		Iskandar, 2000
	Thailand	?	1	Religious		Iskandar, 2000
	US: Florida	N	1	Pet trade		Bartlett, 1967b
<i>Macrolemys temminckii</i>	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004
	France	N	1	Pet trade		Haffner, 1997
	Japan: mainland	N	1	Pet trade		Uchiyama et al., 2002; Yasukawa, 2005
	US: California	N	1	Pet trade	1968	Murphey, 1969; Bury & Luckenbach, 1976; Jennings, 1987a, 2004
<i>Malaclemys terrapin</i>	US: Florida	N	1			Iverson & Eichberger, 1989
	US: California	N	4	Food (2), pet trade (2)	1897, 1943	Vogelsang & Gould, 1900; Taft, 1944; Hildebrand & Prytherch, 1947; Banta & Morafka, 1966; P.R. Brown, 1971; Bury & Luckenbach, 1976; Jennings, 1987a, 2004; Ernst et al., 1994

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Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Illinois	N	1	Pet trade	1973	Dancik, 1974	
	US: Massachusetts	?	5	Intentional (2)	1924, 1968, 1988, 1992 (2)	Babcock, 1926; Hoff, 1982; Cardoza et al., 1993	
	US: Pennsylvania	N	1	Pet trade	1966	McCoy, 1982	
	US: Florida	N	1	Pet trade		Bartlett, 1967b	
	US: New Mexico	N	1	Pet trade	1968	Price & Johnson, 1978; Degenhardt et al., 1996	
	Singapore	N	1			Ng et al., 1993	
	Belgium	N	1			Parent, 1983	
	Germany	N	1			Schlipmann & Geiger, 1998	
	Great Britain	N	1	Pet trade	1986	Young, 1987; D. Frazer, 1989	
	Italy	N	3			Lanza & Corti, 1993, 1996; Ferri, 1996; Luiselli et al., 1997; Sofianidou, 1997b; Razzetti & Sindaco, 2006	
	Netherlands	N	1		1980s	Gubbels, 1992	
	Saudi Arabia	N	1		1989	Gasperetti et al., 1993	
	Balearic Islands	N	4	Pet trade (4)		Lortet, 1887; Alcover, 1979; Alcover & Mayol, 1981; J. Rivera & Arribas, 1993	
	Denmark	N	1	Intentional	1964	J. Christiansen, 1974	

Mauremys leprosa (syn: *Mauremys caspica*)

France	N	3	Pet trade (3)	1980, 1983, 1991	Gemiez & Cheylan, 1987; Bour, 1989; Colin, 1992; Haffner, 1997; C. Keller & Busack, 2001
Germany	N	1			Schlüpmann & Geiger, 1998
Italy	N	3	Pet trade (2)	1983 (2)	Lanza & Corti, 1993, 1996; López Jurado, 1997; Luiselli et al., 1997; Razzetti & Sindaco, 2006
Spain	Y	16	Biocontrol (1), pet trade (3)		Fernández de la Cigüeña, 1989; Gosa & Bergerandi, 1994; C. Keller & Busack, 2001; Pleguezuelos, 2004
France	N	1	Pet trade		Haffner, 1997
Hong Kong	N	5	Medicine, pet trade		Karsen et al., 1998
Japan: mainland	Y	15	Pet trade (15)	Late 1920s, 1990s (2)	Hara, 1986; Hikida et al., 1992; Yasukawa et al., 1996; Yasukawa & Ota, 1999; Ota, 2000; Uchiyama et al., 2002; Goris & Maeda, 2004; Kobayashi & Hasegawa, 2005b; Toda & Yoshida, 2005; Kobayashi et al., 2006b

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Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Japan: Ryukyu Islands	Y	12	Pet trade (12)	1980s (3), 1992 (2), 1998, 1990s (2), 2002, early 2000s	Toyama & Ota, 1991; Hidida et al., 1992; Ota et al., 1994a, 2004a, b; Ota, 1995, 1999, 2000; Yasukawa et al., 1996; Masuno et al., 1998; Nohina et al., 1998; Yasukawa & Ota, 1999; Nakata, 2001; Honda et al., 2002; Goris & Maeda, 2004; Oka, 2004; Shiroma & Ota, 2004; Toda & Yoshida, 2005	Ota & Hamaguchi, 2003
<i>Mauremys reevesii</i> (syn: <i>Chinemys reevesii</i>)	Canada: British Columbia	N	1		1920s	Gregory & Campbell, 1984	
(syn: <i>Chinemys reevesii</i>)	Germany	?	1	Pet trade		Hanka & Joger, 1998	
(syn: <i>Chinemys reevesii</i>)	Guam	N	1	Pet trade	2000	Leberer, 2003	
(syn: <i>Chinemys reevesii</i>)	Indonesia: Timor	N	1	Pet trade		Iskandar, 2000	
(syn: <i>Chinemys reevesii</i>)	Japan: mainland	Y	2			Toda & Yoshida, 2005	
(syn: <i>Chinemys reevesii</i>)	Japan: Ryukyu Islands	Y	2	Pet trade		Masuno et al., 1998; Itô et al., 2000; Ota, 2000; Ota et al., 2004a; Toda & Yoshida, 2005	
(syn: <i>Chinemys reevesii</i>)	Mauritius	N	1	Pet trade	1940	Bour, 1984a, b; Cheke, 1987	
(syn: <i>Chinemys reevesii</i>)	Palau	?	1	Food		Crombie & Pregill, 1999	
(syn: <i>Chinemys reevesii</i>)	US: California	N	1	Pet trade	1990s	Spinks et al., 2003	
(syn: <i>Chinemys reevesii</i>)	US: Illinois	?	3	Pet trade (3)	1971	Dancik, 1974; Anton, 1999	

(syn: <i>Chinemys reevesii</i>)	US: Maryland	N	1	Pet trade	1991	Cooper, 1961
(syn: <i>Chinemys reevesii</i>)	US: Massachusetts	N	1	Pet trade		Cardoza et al., 1993
<i>Mauremys rivulata</i> (syn: <i>Mauremys caspica</i>)	Italy	N	7	Pet trade (7)		Bruno, 1986; Lanza & Corti, 1993, 1996; Luiselli et al., 1997; Sofianidou, 1997b; Razzetti & Sindaco, 2006
<i>Mauremys sinensis</i> (syn: <i>Ocadia sinensis</i>)	FSM	N	1		1999	Buden et al., 2001
(syn: <i>Ocadia sinensis</i>)	Guam	?	1	Pet trade	1990s	Leberer, 2003
(syn: <i>Ocadia sinensis</i>)	Hong Kong	N	1		1940s	Karsen et al., 1998
<i>Mauremys</i> sp.	Germany	N	1			Geiger & Waitzmann, 1996
	Italy	N	3			Bologna et al., 2000; Marangoni, 2000a
<i>Melanochelys trijuga</i> (syn: <i>Geoemyda trijuga</i>)	US: Massachusetts	N	1		1980s	Cardoza et al., 1993
	Chagos Archipelago	?	1			G.C. Bourne, 1886; Laidlaw, 1903; Stoddart, 1971; Dutton, 1981b; Barnett & Emms, 1997
(syn: <i>Nicoira trijuga thermalis</i>)	Maldives Islands	Y	1			Gardiner, 1906; Deraniyagala, 1956; Moutou, 1985
<i>Palea steindachneri</i>	Hong Kong	N	1	Food	1980	Karsen et al., 1998
(syn: <i>Amyda cartilaginea</i>)	Mauritius	Y	1	Pet trade	1920	Bour, 1984a, b; Cheke, 1987; Tonge, 1990; Kabitsch, 2004
(syn: <i>Aspidonectes californiana</i> , <i>Trionyx sinensis</i> , <i>Trionyx spiniferus</i>)	US: California	N	1	Food	1889	Van Denburgh, 1917b; Webb, 1975; Jennings, 2004

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Hawaii	Y	1	Food	Mid-late 1800s	Webb, 1980; McKeown & Webb, 1982; McKeown, 1996	
<i>Pelodiscus sinensis</i>	France	N	1	Pet trade		Haffner, 1997	
	Great Britain	N	1			Arnold & Ovenden, 2002	
	Guam	Y	1	Food	1977	E.W. Campbell & McCoid, 1993a; McCoid, 1993a, 1999; Eldredge, 1994; Leberer, 2003	
	Indonesia	Y	3	Religious (2)		Pritchard, 1979; Ernst & Barbour, 1989; Iskandar, 2000	
	Japan: Ryukyu Islands	Y	13	Food (11)	1909, 1931, 1950s (3), 1962, 1970s (2), 1976 (2), 1979 (2), 1980s	Toyama, 1984a, 1998; Ernst & Barbour, 1989; Ota, 1995, 1999, 2000; Ota & Sato, 1997; Sato et al., 1997; Masuno et al., 1998; Sato & Ota, 1999; Ota et al., 2004a, b; Tanaka, 2004; Toda & Yoshida, 2005; Yasukawa, 2005	Sato & Ota, 2001; Sato, 2006
	Madagascar	N	1			Petit, 1936; Blanc, 1972	
	Malaysia	Y	2	Food, religious		Lim & Das, 1999; Iskandar, 2000; Jensen & Das, 2006	
	Philippines	?	2	Food		Pritchard, 1979; Sy et al., 2004	

Singapore	Y	2	Food, religious	Early 1970s	Pritchard, 1979; Chou & Lam, 1989; Lim & Chou, 1990; Yong, 1990; Lim & Lim, 1992; Ng et al., 1993; Iskandar, 2000
Spain	Y	8	Pet trade (8)	1990s (8)	Mateo, 1997a; Barbadillo et al., 1999; Pleguezuelos, 2004
Thailand	Y	2	Pet, religious		Pritchard, 1979; Thirakhupt & van Dijk, 1994, 1996; Iskandar, 2000
US: Hawaii	Y	1	Food	Mid-late 1800s	Brock, 1947; Oliver & Shaw, 1953; McKeown & Webb, 1982; McKeown, 1996; Kraus, 2002b
US: Maryland	N	1	Food	2003	Harris, 2004
Spain	N	1	Pet trade	1987	Pleguezuelos, 2004
Guadeloupe	Y	1			Lescure, 1979, 1983; Schwartz & Henderson, 1991; Iverson, 1992; Breuil, 2002
Madagascar	N	1		1900	Bour, 1983
Chagos Archipelago	?	1			Gardiner & Cooper, 1907; Boulenger, 1909; Stoddart, 1971; Dutton, 1981b; Bour, 1984a, b; Barnett & Emms, 1997
Glortoso Isles	Y	1			Bour, 1983

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Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Mauritius	N	1		1871	Bour & Moutou, 1982; Bour, 1984a, b; Cheke, 1987; F.W. King & Burke, 1989; Iverson, 1992	
	Seychelles: Silhouette	Y	1		1927	Honegger, 1966; Bour, 1983	
	US: Florida	?	1	Pet trade		Bartlett & Bartlett, 1999; Meshaka et al., 2004a	
<i>Podocnemis expansa</i>	Colombia	Y	3	Food (3)	1940, 1943, 1955	Medem, 1960, 1969; Rueda-Almonacid, 1999	
<i>Podocnemis lewyana</i>	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966	
<i>Podocnemis sextuberculata</i>	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966	
<i>Podocnemis unifilis</i>	Colombia	N	1	Food	1968	Rueda-Almonacid, 1999	
	US: Florida	N	1	Pet trade	1964	W. King & Krakauer, 1966; Bartlett, 1967b	
<i>Pseudemys concinna</i>	Japan: mainland	N	1	Pet trade		Yasukawa, 2005	
	US: California	N	3	Pet trade (3)	1980s (1), 1990s (1)	Jennings, 1987a, 2004; Holland, 1994; Spinks et al., 2003	
	US: Florida	Y	2			Iverson & Etchberger, 1989	
	US: Illinois	N	2	Pet trade	1971	Dancik, 1974	
	US: Maryland	N	3			Cooper, 1965; Manville, 1968; Harris, 1969	
	US: Massachusetts	N	3	Pet trade (1)	1944, 1979, 1991	Graham, 1982; Cardoza et al., 1993	
	US: New York	N	2	Pet trade (2)	1960	Burnley, 1968	

<i>Pseudemys floridana</i> (syn: <i>Pseudemys peninsularis</i>)	US: Texas	Y	1	Pet trade		Conant, 1977
	Japan: mainland	N	1	Pet trade		Yasukawa, 2005
	Spain	N	1	Pet trade	2001	Pleguezuelos, 2004
	US: California	N	1	Pet trade		Jennings, 1987a
	US: Colorado	N	2	Pet trade (1)	1950	Rodeck, 1948; Livo et al., 1998
	US: Florida	N	3			Iverson & Eichberger, 1989; Lazell, 1989a
	US: Illinois	N	1	Pet trade	1971	Dancik, 1974
	US: Massachusetts	N	3		1991, 1992, 1990s	Cardoza et al., 1993
	US: New Mexico	N	1	Pet trade	1994	Stuart, 1995b
	British Virgin Islands	N	1			J. Owen et al., 2005b; Perry & Gerber, 2006
<i>Pseudemys gorzugi</i> <i>Pseudemys nelsoni</i>	Japan: mainland	N	1	Pet trade		Yasukawa, 2005
	US: Florida	?	1			Lazell, 1989a
	US: Texas	Y	1	Pet trade		Rose et al., 1998
<i>Pseudemys</i> sp.	Germany	N	3	Pet trade (3)	1984, 1988	Eckstein & Meinig, 1989; Hanka & Joger, 1998; Schlipmann & Geiger, 1998
	US: Massachusetts	N	2		1982, 1989	Cardoza et al., 1993
	US: Massachusetts	N	1		1990	Cardoza et al., 1993
<i>Rhinoclemmys pulcherrima</i>	US: Illinois	N	1			Anton, 1999

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Siebenrockiella crassicornis</i>	Singapore	N	1			Ng et al., 1993	
<i>Terrapene carolina</i>	Bahamas	?	2	Pet trade (2)		D.S. Lee, 2004, 2005	
	Canada: Ontario	?	7	Pet trade (7)		F.R. Cook, 1984	
	Great Britain	N	1	Intentional		Fitter, 1959	
	Guam	?	4	Pet trade (4)	1991	McCoid, 1992a, 1993a, 1999; Leberer, 2003	
	US: Arizona	N	1	Pet trade	1981	Lazaroff et al., 2006	
	US: California	N	50	Pet trade (50)		Lockley, 1948; Bury & Luckenbach, 1976; Jennings, 1987a, 2004	
	US: Colorado	N	7	Pet trade (7)	1947, 1950, 1970s, 1991, 1995	Rodeck, 1949; Maslin, 1959; Livo et al., 1998	
	US: Hawaii	N	1			Mull, 1987	
	US: Illinois	N	7	Pet trade (7)	1971, 1972, 1980s (3)	Dancik, 1974; Ludwig et al., 1992; Anton, 1999	
	US: Iowa	N	5	Pet trade (5)	1971, 1980s (2), 1990s, 1998	Christiansen, 2001	
US: Kansas	N	2	Pet trade (2)	1993, 1995	Collins, 1994, 1996		
US: Maryland	N	2	Pet trade	1980s	Polley, 1989		
US: Massachusetts	Y	6	Pet trade (1)	1960 (1)	Lazell, 1976; Cardoza et al., 1993		
US: Missouri	N	2	Pet trade (2)		Anderson, 1965		
US: New Mexico	N	3	Pet trade (3)	1953, 1995	Degenhardt et al., 1996; Stuart, 2000		
US: New York	N	2	Pet trade (2)	Early 1960s (2)	Burnley, 1968		

<i>Terrapene ornata</i>	US: Wisconsin	N	2	Pet trade (2)	1923, 1960	R.C. Vogt, 1981
	US: California	N	50	Pet trade (50)	1906, 1925, 1947, 1960, 1963 (2), 1986, late 1980s, 1990 (2), 1991, 1992, 1993, 1995, 1997	Bury & Luckenbach, 1976; Jennings, 1987a, 2004
	US: Colorado	N	16	Pet trade (16)		Livo et al., 1998
<i>Terrapene</i> sp.	US: Illinois	N	2	Pet trade (2)		Ludwig et al., 1992
	US: Massachusetts	N	3		1991 (2)	Lazell, 1976; Cardoza et al., 1993
	US: Virginia	N	1	Pet trade		Ernst et al., 1997
testudinid sp.	US: California	N	1			Dixon, 1967
	New Zealand	N	2	Pet trade	1843, 1913	Thomson, 1922; McCann, 1966; West, 1979
<i>Testudo graeca</i>	Balearic Islands	Y	2	Intentional, pet trade	<1876, 1990s	Boscá, 1877; Maluquer, 1918, 1919; López-Jurado et al., 1979; Alcover & Mayol, 1981; Salvador & Pérez Mellado, 1984; Rivera & Arribas, 1993; Kramer, 1995; Andreu y López-Jurado, 1997; Mateo, 1997a; Palerm, 1997; Salvador & Pleguezuelos, 2002; Mayol, 2003; Pleguezuelos, 2004

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Belgium	N	2			de Wavrin, 1974; Parent, 1983	
	Canary Islands	?	1			Pleguezuelos, 2004	
	Cyprus	?	2	Pet trade (1)	1970s (1)	Demetropoulos & Lambert, 1986; Demetropoulos & Hadjichristophorou, 1995	
	France	N	2	Pet trade	>1800	Lortet, 1887; Fretey, 1975, 1986; Honegger, 1978; Geniez & Cheylan, 1987; Buskirk et al., 2001; Pascal et al., 2006	
	France: Corsica	?	1			Honegger, 1978; Pascal et al., 2006	
	Germany	N	1	Pet trade		Geiger & Waitzmann, 1996	
	Great Britain	N	1	Pet trade	1951	Fitter, 1959; C. Lever, 1977	
	Greece	?	1			Lambert, 1997	
	Greece: Crete	N	1			Strijbosch, 1983; Lambert, 1997; Hofstra, 2000; Buskirk et al., 2001	
	Ireland	N	1	Intentional	1906	Fitter, 1959; J.F.D. Frazer, 1964	

(syn: *Testudo iberica*)

Italy	Y	6	Pet trade (5)	Tortonese & Lanza, 1968; Bruno & Maugeri, 1976; Lanza, 1983a; Bruno, 1986; Stubbs, 1989; Frisenda & Ballasina, 1990; Lanza & Corti, 1993, 1996; Ballasina, 1995; Fattizzo, 1996; Lambert, 1997; Bertolino, 1999; Bologna et al., 2000; Carpaneto, 2000a; Buskirk et al., 2001; Fattizzo & Marzano, 2002
Italy: Sardinia	Y	1		Tortonese & Lanza, 1968; Bruno & Maugeri, 1976; Lanza, 1983a; Bruno, 1986; Stubbs, 1989; Frisenda & Ballasina, 1990; Lanza & Corti, 1993, 1996; Ballasina, 1995; U. Fritz et al., 1996; Lambert, 1997; Buskirk et al., 2001; Razzetti et al., 2006
Italy: Sicily	Y	2		Tortonese & Lanza, 1968; Bruno, 1970, 1986; Bruno & Maugeri, 1976; Stubbs, 1989; Frisenda & Ballasina, 1990; Lambert, 1997

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Malta	Y	3	Food, intentional, pet trade	1964	Gullia, 1890, 1914; Lanfranco, 1964; Lanza, 1973; Bruno & Maugeri, 1976; Savona-Ventura, 1985; Stubbs, 1989	
	Spain	Y	7		1949, 1950, 1951, 1953, 1954, 1987	Boscá, 1877; Lortet, 1887; Valverde, 1967; López-Jurado et al., 1979; Casaldueiro, 1986; López-Higuera et al., 1989; J. Rivera & Arribas, 1993; Andreu y López-Jurado, 1997; Mateo, 1997a; Barbadillo et al., 1999; Balmori, 2000; Campos-Sánchez et al., 2000; Buskirk et al., 2001; Salvador & Pleguezuelos, 2004	López-Jurado et al., 1979; Braza et al., 1981; Andreu & Villamor, 1986; Cobo & Andreu, 1986, 1988; Roca et al., 1986, 1988a, b; Sanchez et al., 1986; Blasco et al., 1988; Castanedo et al., 1991; C. Keller et al., 1993, 1997, 1998; Díaz-Paniagua et al., 1995, 1996, 1997, 2001, 2006; Giménez et al., 1999; Alvarez et al., 2000; Andreu et al., 2000; Pérez et al., 2002, 2004; Roques et al., 2004; Anadón et al., 2005, 2006a, b
<i>Testudo hermanni</i>	Austria	Y	4	Intentional (3), pet trade (1)	1971	Eiselt, 1961; Sochurek, 1978; Street, 1979; Cabela, 1990; Grillitsch, 1993	
	Balearic Islands	Y	1	Food		López-Jurado et al., 1979; Alcover & Mayol, 1981; Rivera & Arribas, 1993; Esteban et al., 1994; Kramer, 1995; Bour, 1997; Lorente et al., 1997b; Barbadillo et al., 1999; Pleguezuelos, 2004	Raxworthy, 1984; Soler-Massana et al., 2001; H.U. Schmidt, 2004a, b, 2006; Bertolero, 2005

Belgium	N	1				Parent, 1983
Canary Islands	?	1				Pleguezuelos, 2004
Cyprus	?	1	Pet trade			Demetropoulos & Hadjichristophorou, 1995
France	Y	3		<1939		Arnoult, 1958; Fretey, 1975, 1986; Honegger, 1978; Street, 1979; J. Rivera & Arribas, 1993
Germany	N	2	Pet trade (2)	1980s, 1984		Eckstein & Meinig, 1989; Münch, 1992; Geiger & Waitzmann, 1996
Italy	?	6	Intentional (3), pet trade	1994 (1), 1990s (2)		Corti et al., 1997; Bertolino, 1999; Fattizzo & Marzano, 2002; Corti et al., 2006; Razzetti et al., 2006
Malta	?	1				Bour, 1997; Cheylan, 2001
Slovenia	?	1				Tome, 1997
Spain	Y	5		1979, 1980		López-Jurado et al., 1979; Bertolero et al., 2005 García-P. et al., 1989; J. Rivera & Arribas, 1993; Bour, 1997; Lorente et al., 1997b; Barbadiño et al., 1999; Salvador & Pleguezuelos, 2002
Austria	N	1	Pet trade	1972		Sochurek, 1978
Egypt	Y	1	Intentional	Late 1990s		Perälä, 2001
Italy	N	1	Pet trade			Bagnoli & Carpaneto, 2000

Testudo horsfieldii

Testudo kleinmanni

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Testudo marginata</i>	Cyprus	?	6	Pet trade (3)	1970s (1), 1990s (2)	Demetropoulos & Lambert, 1986; Hadjisterkotis & Reese, 1994; Demetropoulos & Hadjichristophorou, 1995	
	Greece: Crete	N	1			Hofstra, 2000	
	Italy	Y	8	Pet trade		Tortonese & Lanza, 1968; Honegger, 1978; Lanza, 1983a; Frisenda & Ballasina, 1990; Lanza & Corti, 1993, 1996; Ballasina, 1995; Sofianidou, 1997c; Bologna et al., 2000; Campanato, 2000b; Bringsøe et al., 2001; Fattizzo & Marzano, 2002; Razzetti et al., 2006	
	Italy: Sardinia	Y	1			Tortonese & Lanza, 1968; Honegger, 1978; Lanza, 1983a; Frisenda & Ballasina, 1990; Lanza & Corti, 1993, 1996; Ballasina, 1995; U. Fritz et al., 1995; Sofianidou, 1997c; Böhme, 2000; Bringsøe et al., 2001; Vinke & Vinke, 2004; Razzetti et al., 2006	

Malta	N	1				Gulia, 1890, 1914; Lanza, 1973; Bringsøe et al., 2001
<i>Trachemys decussata</i>	N	1	Pet trade	1997		D.S. Lee, 2004, 2005
Bahamas	N	1		1875		Seidel & Franz, 1987; Dunson & Seidel, 1986; Seidel, 1990, 2003
Cayman Islands	Y	1				Alderton, 1988; Seidel, 1988, 1996
US: Florida	N	1	Pet trade	1964		W. King & Krakauer, 1966
US: New Mexico	N	1	Pet trade	1995		Stuart, 2000
Aruba	?	2				van Buurt, 2005
Australia	Y	4	Pet trade (4)			Burgin & Emerton, 1997; K. Griffiths, 1997; Low, 2003; O'Keefe, 2005; S. Wilson, 2005
Austria	Y	8	Pet trade (7)	1980s (3), 1988, 2005 (4)		Sochurek, 1978; Lutschinger, 1989; Cabela, 1990; Manzano, 2000; Bringsøe, 2001a, 2002a; Kaltenegger, 2006
Bahamas	Y	2	Pet trade (2)	1970s (2)		D.S. Lee & Ross, 2001; Lee & Carey, 2001
Bahrain	Y	1	Pet trade	1986		Mealey et al., 2002; D.S. Lee, 2004, 2005
Balearic Islands	Y	2	Pet trade			Leviton et al., 1992; Gasperetti et al., 1993
						J. Rivera & Arribas, 1993; Avellà, 1998; Mas & Perelló, 2001; Pleguezuelos, 2004

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Belgium	?	70	Pet trade	1970s	Percy, 1995, 1998, 2000; Jooris et al., 1998; Jooris, 2000; Bringsøe, 2001a, 2002a; Percy & Percy, 2002a	
	Bermuda	Y	4	Pet trade (4)	1980s (4)	C. Lever, 2003; Davenport et al., 2005; Bacon et al., 2006b	
	Brazil	Y	1			Servan & Arvy, 1997	
	British Virgin Islands	Y	15	Pet trade (15)	1980s, 1990s, 2000s, 2004	J. Owen et al., 2005b; Perry & Gerber, 2006; Perry et al., 2007	
	Canada: British Columbia	?	1			Gregory & Gregory, 1999; Orchard, 2000	
	Canary Islands	?	1	Pet trade		Rodríguez Luengo, 2001; Pleguezuelos, 2004	
	Cayman Islands	Y	1			C. Lever, 2003	
	Chile	Y	1	Pet trade		Núñez et al., 2002; Iriarte et al., 2005	
	CNMI	Y	1	Pet trade		Rodda et al., 1991; McCoid, 1999; S.R. Vogt & Williams, 2004	
	Czech Republic	?	1	Pet trade	1980s	Bringsøe, 2001a	
	Denmark	N	4	Intentional, pet trade (3)	1964	J. Christiansen, 1974; Bringsøe, 1997, 2001a, 2002a, b; Fog et al., 1997; Jorgensen, 1999; Jensen, 2002	

Egypt	Y	2	Pet trade (2)	1992, 1995	Saleh, 1997; Baha el Din, 2006	Devaux, 2000; Cadi & Joly, 2003, 2004; Cadi et al., 2004; Dupré et al. 2006; Prévot-Julliard et al., 2006
France	Y	309	Pet trade (7)		Fretey, 1986; Colin, 1992; Haffner, 1997; Servan & Arvy, 1997; Arvy & Servan, 1998; Hermanns & Nizet, 1998; Arets, 2000; Bringsøe, 2002a; Cadi & Bertrand, 2003; Levasseur & Faucheux, 2003; Pascal et al., 2006	
French Polynesia	Y	1			Servan & Arvy, 1997	
FSM	N	1	Pet trade	Late 1980s	Buden, 2000a; Buden et al., 2001	
(syn: <i>Chrysemys picta</i> , <i>Pseudemys ornata</i>)	Y	314	Pet trade (14)	1970s, 1980 (2), 1982, 1983, 1984 (4), 1987, 1988 (3), late 1980s (2), 1980s, early 1990s	Gerstner et al., 1978; Podloucky, 1985; Lautermann, 1986; Neseemann, 1986; Anonymous, 1987; Klewen & Müller, 1988; Eckstein & Meinig, 1989; Kordges et al., 1989; Münch, 1992; Ernst et al., 1994; Bammerlin & Bitz, 1996; Schlipmann, 1996; Arvy, 1997; Dalbeck et al., 1997; Härtel & Plesker, 1997; Budde, 1998; Hanka & Joger, 1998; Podloucky, 1998; Schlipmann & Geiger, 1998; Bringsøe, 2001a, 2002a; Folger, 2001; Pieh & Laufer, 2006	Thiesmeier & Kordges, 1990

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	Great Britain	N	3	Pet trade (3)	1960, 1986, 1990s	Yalden, 1965; Young, 1987; Gillett, 1988; Ernst, 1990; Daniels, 1994; Beebee & Griffiths, 2000; Bringsøe, 2001a, 2002a; Arnold & Ovenden, 2002	
	Greece	Y	2	Pet trade (2)	1980s, 1990s	Dimitropoulos, 1989; Bringsøe, 2001a, 2002a; Bruekers et al., 2006	
	Greece: Crete	?	2	Pet trade		Schepp, 1996; Hofstra, 2000; Bringsøe, 2001a, 2002a	
	Guadeloupe	Y	4	Pet trade (4)		Schwartz & Thomas, 1975; Lescure, 1979; Schwartz & Henderson, 1988, 1991; Breuil, 2002	
	Guadeloupe: Marie-Galante	Y	1	Pet trade		Breuil, 2002	
	Guam	Y	1	Pet trade	1970s	Rodda et al., 1991; McCoid, 1992b, 1993a, 1999; Eldredge, 1994; Leberet, 2003; S.R. Vogt & Williams, 2004	
	Guyana	Y	1			Servan & Arvy, 1997	
	Hong Kong	Y	9	Pet trade (6), religious (3)		Hill & Phillips, 1981; Bringsøe, 1991, 2001a; Herrmann et al., 1996; Karsen et al., 1998; Cheung, 2001	

Hungary	?	10		Puky et al., 2004
India	?	1		Lim & Das, 1999
Indonesia	Y	5	Pet trade	U. Fritz & Gaulke, 1997; Iskandar, 2000; Bringsøe, 2001a
Israel	?	3	Pet trade (3)	Gasith & Sidis, 1983; Bouskila, 1986; F.W. King & Burke, 1989; Bringsøe, 2001a
Italy	Y	59	Pet trade (59)	Bruno, 1986; Lanza & Corti, 1993, 1996; Scali, 1995; Ferri, 1996; Generani & Danini, 1996; Lapini et al., 1996, 1999; Viora, 1996; Luiselli et al., 1997; Bertolino, 1999; Gianaroli et al., 1999; Bologna et al., 2000; Ferri & Di Cerbo, 2000; Fracasso & Bonato, 2000; Fracasso et al., 2000; Marangoni, 2000b; Petterino et al., 2001; Bringsøe, 2002a; Caldonazzi et al., 2002; Fattizzo & Marzano, 2002; Fiacchini, 2003; Crucitti et al., 2004; Razzetti et al., 2006

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
(syn: <i>Chrysemys scripta elegans</i>)							
	Japan: mainland	Y	11	Pet trade (4), zoo trade (1)	1960s (2), 1970s (2)	Hara, 1986; I. Uchida, 1989; Ernst, 1990; Utsunomiya et al., 1996; Ota, 2000; Ter Borg, 2000; Uchiyama et al., 2002; Goris & Maeda, 2004; Nishikawa et al., 2005; Toda & Yoshida, 2005; Yasukawa, 2005	Ishida et al., 2004; H. Hasegawa & Asakawa, 2004
	Japan: Ogasawara Islands	Y	1			Toda & Yoshida, 2005	
	Japan: Ryukyu Islands	Y	8	Pet trade (8)	1990s (2), 2003, 2004	I. Uchida, 1989; Ernst, 1990; Ota, 1995, 1999, 2000; Masuno et al., 1998; Toyama, 2002; Goris & Maeda, 2004; Oka, 2004; Ota et al., 2004a; Shiroma & Ota, 2004; Toda & Yoshida, 2005	Ishida et al., 2004
	Kenya	?	3			Hennig, 2004	
	Malaysia	Y	1	Pet trade		Moll, 1995; Arvy, 1997; Cox et al., 1998; Chahard et al., 1999; Lim & Das, 1999; Bringsøe, 2001a	
	Martinique	Y	1			Servan & Arvy, 1997; Breuil, 2002	

Netherlands	N	97	Pet trade (15)	1980s, 1985 (4), 1986, 1988, 1989 (3), 1990 (2)	Smit & Zuidervijk, 1990b; Melchers & Timmermans, 1991; Gubbels, 1992; Arvy, 1997; Ter Borg, 2000; Bringsøe, 2001a, 2002a	Feldman, 1992
New Zealand	N	8	Pet trade (8)	1970s (5), 1999, 2004	West, 1979; M. Thomas & Hartnell, 2000; Feldman, 2005; Hoskins, 2005	
Canada: Ontario	Y	1			Harding, 1997	
Panama	Y	1			Moll, 1995	
Paraguay	N	1			Vinke & Vinke, 2006	
Poland	?	15	Pet trade (15)	1990s (15)	Mitrus, 2000; Najbar, 2001	
Portugal	?	3	Pet trade (3)		Godinho et al., 1999; Bringsøe, 2001a, 2002a; Ferrand de Almeida et al., 2001	
Réunion	Y	1	Pet trade		Bour & Moutou, 1982; Servan & Arvy, 1997	
Saudi Arabia	Y	1			Servan & Arvy, 1997	
Seychelles	?	2		1990s (2)	Gerlach, 1997	
Singapore	Y	1	Pet trade		Lim & Chou, 1990; Lim & Lim, 1992; Ng et al., 1993; Cox et al., 1998; Lim & Das, 1999	
Slovenia	?	5			Tome, 1997; Bringsøe, 2001a	

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
(syn: <i>Chrysemys scripta</i> , <i>Pseudemys scripta</i>)	South Africa	Y	9	Pet trade (9)		Newbery, 1984; Branch, 1988; de Moor & Bruton, 1988; Bruton & van As, 1986; Boycott & Bourquin, 2000; Bourquin, 2004	
	South Korea	Y	1	Pet trade		Platt & Fontenot, 1992	
	Spain	Y	183	Pet trade (30)	1990s (4)	García-Paris & Martín Albadalejo, 1987; García-Paris et al., 1989; Rivera & Arribas, 1993; da Silva & Blasco, 1995; da Silva, 1995; Llorente et al., 1995; Mateo, 1997a; Barbadillo et al., 1999; Gómez-Cantarino & Lizana, 2000; Martínez-Silvestre & Cerradello, 2000; Bertolero, 2001; Bringsøe, 2002a; Salvador & Pleguezuelos, 2002; Rivera & Sáez, 2003; Cordero Rivera & Ayres Fernández, 2004; Pleguezuelos, 2004	Casanovas, 1997; Martínez-Silvestre et al., 1997; de Roa & Roig, 1998; Capalleras & Carretero, 2000; Bertolero & Canicio, 2000; Lacomba Andueza & Sancho Alcayde, 2004; Ayres & del Pozo, 2006
	Sri Lanka	Y	1			Arvy, 1997; Servan & Arvy, 1997	
	St. Maarten	Y	1	Pet trade		Powell et al., 2005	

Sweden	N	3	Pet trade (3)	1975, 1977, 1980	Nilsson & Andrén, 1986; Ahlén et al., 1995; Fog et al., 1997; Bringsøe, 2001a, 2002a
Switzerland	?	40	Pet trade (40)		A. Keller et al., 1993; Bringsøe, 2001a; Mosimann & Cadi, 2004
Taiwan	Y	8	Pet trade, religious	1980s	Chen & Lue, 1998; Ota, 2000; Lue et al., 2003
Thailand	Y	1	Pet trade		Moll, 1995; Thirakhupt & van Dijk, 1994, 1996; Cox et al., 1998; Chand et al., 1999; Farkas, 1999; Bringsøe, 2001a
Trinidad	?	1			J.C. Murphy, 1997
Turkey	?	1			Parham & van Leuvan, 2002
U.S. Virgin Islands	?	1	Pet trade		Platenberg & Boulon, 2006
US: Arizona	Y	4	Pet trade (3)	1983	Hulse, 1980; Stebbins, 1985; Jennings, 1987d; Brennan & Holycross, 2005; Lazaroff et al., 2006
US: California	Y	25	Pet trade (14)	1920s (2), 1935 (3), 1960s	Hanna & Clark, 1925; C. Grant, 1936; Bury & Luckenbach, 1976; Stebbins, 1985; De Lisle et al., 1986; Jennings, 1987a, 2004; Holland, 1994; Bringsøe, 2001a; Spinks et al., 2003; Stitt et al., 2004; Bettelheim et al., 2006; Fidenci, 2006
					Leatherman & Jennings, 2007

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Colorado	N	8	Pet trade (8)	1913, 1984, 1991 (2), 1992, 1994, 1995, 1996	Rodeck, 1948; Livo et al., 1998	
	US: Connecticut	Y	2	Pet trade (1)	1930	DeGraaf & Rudis, 1983; Klemens, 1993; Watkins-Colwell et al., 2006	
	US: District of Columbia	Y	1			Ernst, 1990	
	US: Florida	Y	24	Pet trade (24)	1950s, 1960s, 1964, 1996	W. King & Krakauer, 1966; Bartlett, 1967b; L.D. Wilson & Porras, 1983; Ashton & Ashton, 1985; Iverson & Eichberger, 1989; Hutchison, 1992; Butterfield et al., 1994b, 1997; Duquesnel, 1996; Bartlett & Bartlett, 1999; Meshaka et al., 2000, 2004a; Townsend et al., 2002; Johnston & Johnston, 2003a, b; Ehret & Parker, 2005; Krysko & Sheehy, 2005; Aresco & Jackson, 2006; Enge et al., 2007; H.T. Smith et al., 2007b	Emer, 2004
	US: Hawaii	Y	1	Pet trade	1980	Devick, 1991; McKeown, 1996; Kraus & Duvall, 2004	

US: Illinois	Y	21	Pet trade (3)	1960s (2), 1973	Dancik, 1974; Ludwig et al., 1992; A.K. Wilson, 1994; Anton, 1999
US: Iowa	N	2	Pet trade (2)	1978, 1989	Christiansen, 2001
US: Maine	?	2	Pet trade (2)		Albright, 1999
US: Maryland	Y	11	Pet trade (3)	1930s, 1957, 1960s (2)	M.F. Groves, 1940; Mansueti, 1941a, b; McCauley, 1945; Cooper, 1959, 1961, 1965; Nemuras, 1964; Harris, 1966, 1969, 1975; Nemuras & Spathawk, 1966; J.D. Groves, 1972; Norden, 2005
(syn: <i>Chrysemys scripta</i>)					
US: Massachusetts	Y	15	Pet trade (15)	1970s, 1979, mid-1980s, 1983, 1986, 1988, 1989 (2), 1990, 1991 (3), 1992, 1993	Lazell, 1976; Cardoza et al., 1993
US: Michigan	Y	5	Pet trade (5)	Early 1920s, 1950s, 1972, early 1970s, 1993	Edgren, 1943, 1948; Gordon & Fowler, 1961; Holman, 1994; Harding, 1997
US: Nebraska	N	1	Pet trade		Ballinger & Lynch, 1999
US: New Jersey	Y	2	Pet trade	<1976	Mondrosch, 1979; Stein et al., 1980; Iverson, 1986

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: New Mexico	Y	10	Pet trade (10)	1970s, 1990s, 1998	Degenhardt & Christiansen, 1974; Stuart, 1995b, c, 2000; Degenhardt et al., 1996	
	US: New York	Y	7	Pet trade (7)	1953, 1962, 1963, 1969, 1971	Burnley, 1968; Schlauch, 1969, 1972; Klemens, 1985, 1993	
	US: North Carolina	Y	5	Pet trade (5)		E.E. Brown, 1992; Palmer & Braswell, 1995	
	US: Ohio	Y	2		1960s (1)	Novotny, 1997; McKenna & Tramer, 2001	
	US: Oregon	Y	2	Pet trade (2)		Storm & Leonard, 1995	
	US: Pennsylvania	Y	2	Intentional, pet trade	1957	Cooper, 1959; Manchester, 1982; Iverson, 1986	
	US: South Carolina	Y	1	Pet trade	1995	Platt & Snyder, 1996	
	US: Virginia	Y	17	Pet trade (4)		Mitchell, 1994; D'Alessandro & Ernst, 1995; Ernst et al., 1997; Mitchell, 2004, 2005	
	US: Washington	Y	3	Pet trade (2)		K.R. McAllister, 1995; Storm & Leonard, 1995; Hays et al., 1999	
	US: Wisconsin	?	1	Pet trade	1947	Edgren, 1948; Cochran et al., 1987	
	Bahamas	Y	2			Groombridge, 1982; Seidel & Adkins, 1987; Seidel, 1988; D.S. Lee & Ross, 2001	Hodsdon & Pearson, 1943; D.G. Campbell, 1978
	<i>Trachemys stejnegeri</i> (syn: <i>Chrysemys malonei</i> , <i>Pseudemys malonei</i> , <i>Trachemys malonei</i>)						

Dominica	Y	1				U. Fritz, 1991; Seidel, 1996
Guadeloupe	Y	1				Breuil, 2002
Guadeloupe: Marie-Galante	Y	1				Seidel, 1988; Ernst & Seidel & Adkins, 1987 Barbour, 1989; Breuil, 2002
Puerto Rico: Culebra	?	1				Seidel, 1989
Puerto Rico: Vieques	N	1		1982		Seidel, 1988
US: Florida	N	1		1943		Hodsdon & Pearson, 1943; W. King & Krakauer, 1966; D.G. Campbell, 1978
(syn: <i>Chrysemys malonei</i> ; <i>Pseudemys malonei</i>)						
<i>Trachemys terrapen</i> (syn: Bahamas)	Y	2				Pritchard, 1979; D.G. Campbell, 1978; J.P. Ross, 1982
<i>Chrysemys felis</i>						Groombridge, 1982;
<i>Pseudemys felis</i>						Seidel & Adkins, 1987;
<i>Trachemys felis</i>						Seidel, 1988, 1996; D.S. Lee & Ross, 2001
<i>Trachemys</i> sp.						Iskandar, 2000
Indonesia: Java	Y	1			Pet trade	Franz et al., 1993; Seidel, 1996
Bahamas	Y	1		1910s		
Guam	N	1		1980s		McCoid, 1993a
New Zealand	N	1		1903		Thomson, 1923; West, 1979
CROCODILIANS						
<i>Alligator mississippiensis</i>	N	1		1995		E. Carey, 2002; D.S. Lee, 2004, 2005
Canary Islands	N	1			Pet trade	Pleguezuelos, 2004

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
	US: Arizona	N	5	Exhibit (1), intentional (1), pet trade (1)	1948, 1949	Hock, 1954; Funk, 1963	
	US: California	N	3	Exhibit (2)	1930s (2)	Hock, 1954; Glaser, 1970; Bury & Luckenbach, 1976; Vitt & Ohmart, 1978; Jennings, 1987a, 2004	
	US: Colorado	N	2	Pet trade, zoo trade	1978, 1991	Livo et al., 1998	
	US: Oklahoma	N	2		1940s	Blair, 1950	
	US: Pennsylvania	N	2		1930s (2)	McCoy, 1982	
	US: Virginia	N	5	Intentional (1)	1969, 1974, 1978, 1980, 1982	Mitchell, 1990, 1994	
<i>Caiman crocodilus</i>	US: West Virginia	N	3	Pet trade (3)	1928 (1)	Green & Pauley, 1987	
	Canary Islands	N	1	Pet trade		Pleguezuelos, 2004	
	Colombia: Isla de San Andrés	?	1			Rueda-Almonacid, 1999	
	Cuba: Isla de la Juventud	Y	1	Intentional	1959	Varona, 1976, 1981; Garrido & Jaume, 1984; Escobar Herrera, 1995; Estrada & Ruibal, 1999	Varona, 1980; Groombridge, 1982
	Puerto Rico	Y	1	Pet trade	1950s–1960s	Schwartz & Henderson, 1985, 1991; R. Thomas & Jøglar, 1996; R. Thomas, 1999	

Puerto Rico: Vieques	?	1	Pet trade	1950s–1960s	R. Thomas, 1999
US: Arizona	?	1			Howland, 1996
US: California	N	2	Pet trade (2)		Bury & Luckenbach, 1976; Jennings, 1987a, 2004
(syn: <i>Caiman sclerops</i>) US: Florida	Y	5	Pet trade (5)	Late 1950s	W. King & Krakauer, 1966; Bartlett, 1967a, 1994a; Crowder, 1974; Ellis, 1980; L.D. Wilson & Porras, 1983; Ashton & Ashton, 1985; Dalrymple, 1994; Butterfield et al., 1997; Bartlett & Bartlett, 1999; Meshaka et al., 2000, 2004a
(syn: <i>Caiman sclerops</i>) US: Illinois	N	2	Pet trade (2)	1972, 1973	Dancik, 1974
US: Iowa	N	1	Pet trade		Christiansen, 2001
US: Massachusetts	N	1		1989	Cardoza et al., 1993
US: Virginia	N	4		1964, 1978, 1982	Mitchell, 1994; D'Alessandro & Ernst, 1995; Ernst et al., 1997
<i>Crocodylus acutus</i> US: Virginia	N	1	Intentional	1976	Mitchell, 1994
<i>Crocodylus niloticus</i> South Africa	?	1			Bruton & van As, 1986
<i>Crocodylus porosus</i> Japan; Ryukyu Islands	?	1	Exhibit (2)	2000 (3)	Pleguezuelos, 2004 Ota, 1999
<i>Crocodylus rhombifer</i> Canary Islands	N	1	Pet trade		Pleguezuelos, 2004

(continued)

Table A.1 (continued)

Taxon	Locality introduced	Success?	Number	Pathway	Dates	References	Ecology/impacts/genetics
<i>Melanosuchus niger</i>	Colombia	N	1	Intentional	1943	Medem, 1960; Rueda-Almonacid, 1999	
crocodilian sp.	Spain	N	1	Pet trade	1989	J. Rivera & Arribas, 1993	
	US: Indiana	N	1			Minton, 1972	

Appendix B: Table of Erroneous and Uncertain Introduction Claims

Table Structure and Content

In addition to the questionable ancient introductions discussed under Appendix A, Section 2 the literature contains a number of claimed herpetological introductions that are either uncertain or invalid. Claims are uncertain either because the original claim was noted to be questionable and hasn't subsequently been clarified or because an original claim has subsequently been demonstrated to be false or unreliable. Many of the claimed introductions presented here are clearly erroneous, others are speculative, a few are reasonable but insufficiently resolved to justify inclusion in the primary database. Erroneous claims already corrected in the literature are included here so as to save other researchers the effort of independently re-discovering the corrections or missing them altogether. Other corrections to clearly erroneous claims appear here for the first time (e.g., a number of *Emoia* species claimed by C. Lever [2003] to be introduced). Several of the entries in Table B.1, however, consist of speculative claims of introduction for which no compelling evidence is yet presented. In each case I cite countervailing arguments and evidence, if available. In some instances, the claims are not entirely unreasonable and no countervailing argument has explicitly appeared in the literature but the evidence at present is not sufficiently compelling to warrant their inclusion with the better-supported examples collected in Appendix A. The fields in this table include species, locality for which the introduction is claimed, citations for this claim, best estimate of the claim's validity, reason or rationale for rejecting or questioning the claim, and authority for refuting or questioning the claim. Obviously, in cases wherein the same citation appears in the fields presenting and questioning the claim it is because that literature source raised the reasonable possibility of introduction but lacked sufficient evidence to clearly demonstrate or refute it.

Table B.1 Database of erroneous and uncertain claims of introduction

Species	Claimed locality of introduction	Source for claimed introduction	Valid?	Reason invalid	Evidence questioning, correcting, or providing evidence against claim for introduction
FROGS					
<i>Boophis tephraeomystax</i>	Comoros	Meirte, 1999b, 2004	N	Misidentification of undescribed endemic species	Vences et al., 2003b
<i>Bufo bufo</i>	Japan: Ogasawara Islands	Lever, 2003	N	Apparent misidentification of <i>Bufo marinus</i>	M. Toda, personal communication, 2007
<i>Bufo calamita</i>	Ireland	Macdougald, 1942; J.P.F. Wilson, 1986; D. Frazer, 1989	?	Uncertain if introduced	MacDougald, 1942; Beebee, 1984; D. Frazer, 1989; Gleed-Owen et al., 1999
<i>Bufo melanostictus</i>	Indonesia: Bali	Church, 1960	?	Population recently established but unclear if due to humans	No evidence presented implicating humans
<i>Bufo marinus</i>	Louisiana	Eastel, 1981; Lever, 2001, 2003	N	Misinterpreted locality record	Eastel (1981) claims species established in Louisiana, citing MacLean et al. (1977) as stating the species is established at Grande Terre. But MacLean et al. is a checklist of West Indian herp records and refer to the Grande Terre of Guadeloupe. Claim repeated by Lever (2001, 2003) without correction. Bishop Museum catalogue
<i>Dendrobates leucomelas</i>	US: Hawaii	Benson, 1999	N	Animal captive-reared and given to museum upon death	
<i>Eleutherodactylus lentus</i>	U.S. Virgin Islands: St. John and St. Thomas	MacLean, 1982	?	Uncertain if introduced	No evidence presented for claim
<i>Eleutherodactylus martinicensis</i>	US: Hawaii	Kraus et al., 1999	N	Misidentification of <i>Eleutherodactylus coqui</i>	Kraus & Campbell, 2002

<i>Eleutherodactylus urichi</i>	Guyana, Venezuela	Lescure, 1983	N	Misidentification of native <i>Eleutherodactylus</i> spp.	Kaiser et al., 1994
<i>Hyla gratiosa</i>	US: Maryland	Anderson & Dowling, 1982	?	Apparently native	Arndt & White, 1988
	US: New Jersey	Black & Gosner, 1958	?	Apparently native	Arndt & White, 1988
<i>Hyla squirella</i>	Bahamas	Barbour, 1904, 1914; Schwartz, 1968b	N	Misidentification of <i>Osteopilus septentrionalis</i>	Crombie, 1972
<i>Mantidactylus granulatus</i>	Comoros	Meirte, 1999b, 2004	N	Misidentification of undescribed endemic species	Vences et al., 2003b
<i>Rana aurora</i>	Canada: Queen Charlotte Is.	Ovaska et al., 2002	?	Uncertain if introduced	Ovaska et al., 2002
<i>Rana catesbeiana</i>	Uruguay	Amestoy et al., 1998	?	Language ambiguous	Use of "introduced" in this article refers only to importation but not release/escape into the wild
<i>Rana clamitans</i>	US: Hawaii	Tinker, 1938; Oliver & Shaw, 1953; Hunsaker & Breese, 1967	N	Misidentification of <i>Rana catesbeiana</i>	McKeown, 1996
<i>Rana lessonae</i>	France	Pagano et al., 2001c; Pascal et al., 2006	?	Uncertain if introduced or relict	Pagano et al., 2001c; Daf et al., 2006
<i>Rhombophryne tessudo</i>	Réunion	Guibé, 1978	N	Mistaken locality record	Glaw & Vences, 2002
<i>Scinax rubra</i>	St. Maarten	Schwartz & Henderson, 1991; Malhotra & Thorpe, 1999; Lever, 2003	N	Misidentification of <i>Osteopilus septentrionalis</i>	Powell et al., 1992; Powell & Henderson, 2003
SALAMANDERS					
<i>Necturus maculosus</i>	US: New York (Hudson River)	S.C. Bishop, 1941	?	Probably native	R.E. Schmidt et al., 2004
<i>Taricha granulosa</i>	US: Idaho	Stebbins, 1951; Nussbaum & Brodie, 1971; Nussbaum et al., 1983; Monello & Wright, 1997	?	Likely native	Kuchta & Tan, 2005

(continued)

Table B.1 (continued)

Species	Claimed locality of introduction	Source for claimed introduction	Valid?	Reason invalid	Evidence questioning, correcting, or providing evidence against claim for introduction
LIZARDS					
<i>Anolis sagrei</i>	Central America	Conant, 1975	?	Unclear if introduced by humans	Neill & Allen, 1962; Lee, 1992
<i>Brachylophus fasciatus</i>	Tonga	Pregill & Steadman, 2004	N	Native	Burns et al., 2006
<i>Fureifer pardalis</i>	Réunion	Bourgat, 1967, 1972; J. Vinson & Vinson, 1969	?	Uncertain if introduced	Raxworthy et al., 2002
<i>Emoia adpersa</i>	American Samoa	Lever, 2003	N	Native	W.C. Brown, 1991
<i>Emoia atrocostata</i>	Philippines	W.C. Brown & Alcalá, 1970; Lever, 2003	N	Native	W.C. Brown, 1991
<i>Emoia caeruleo-cauda</i>	Fiji	W.C. Brown, 1991; Zug, 1991; Lever, 2003	?	May be native	Zug & Ineich, 1997
(syn: <i>Emoia callistica</i>)	Guam	Lever, 2003	N	Native	W.C. Brown, 1991
<i>Emoia jakati</i>	New Caledonia	W.C. Brown, 1956; Lever, 2003	N	Mistaken ID or erroneous locality information	Bauer & Sadler, 2000
<i>Emoia lawesii</i>	FSM	Buden, 2000b; Lever, 2003	N	Part of native range	W.C. Brown, 1991
<i>Emoia nigra</i>	American Samoa	Lever, 2003	N	Native	W.C. Brown, 1991
<i>Emoia samoense</i>	American Samoa	Lever, 2003	N	Native	W.C. Brown, 1991
<i>Emoia slevini</i>	Guam	Lever, 2003	N	Native	W.C. Brown, 1991
<i>Emoia trossula</i>	Cook Islands	Lever, 2003	N	Probably native	Crombie & Steadman, 1986; W.C. Brown, 1991
<i>Euleptes paea</i> (syn: <i>Phyllodactylus europaeus</i>)	Malta	Savona-Ventura, 1974	N	Never occurred at this location; claim is a misattribution	Giglioli, 1896; Despott, 1915

<i>Furcifer pardalis</i>	Réunion	Bourgat, 1967, 1970, 1972; Cheke, 1987; Raselimanana & Vences, 2003	?	May be native	Raxworthy et al., 2002
<i>Gehyra oceanica</i>	various Pacific Islands	Lever, 2003	N	Evidence suggests species native	Fisher, 1997
<i>Gymnophthalmus underwoodi</i>	Guadeloupe	Schwartz & Thomas, 1975	N	Likely native	Breuil, 2002
<i>Hemidactylus frenatus</i>	St. Vincent CNMI	Schwartz & Thomas, 1975 Rodda et al., 1991	N ?	Likely native Uncertain if introduced	Corke, 1992 Pregill, 1998
<i>Hemidactylus gar-notii</i>	Guam	Rodda et al., 1992; McCoid, 1993a, 1999	?	Uncertain if introduced	Pregill, 1998
<i>Hemidactylus gar-notii</i>	Brazil	Museum specimen cited in Kluge & Eckardt, 1969	?	Probably based on incorrect locality data	Species not listed subsequently as member of Brazilian fauna
	Peru	Museum specimen	?	Probably based on incorrect locality data	Kluge & Eckardt, 1969
<i>Hemidactylus</i> sp. (syn: <i>Hemidactylus frenatus</i> , <i>H. mabouia</i> , <i>H. mercatorius</i>)	Ascension Is.	Loveridge, 1959, 1961; Ashmole & Ashmole, 1997, 2000	?	Uncertain if introduced because species ID needs verification (<i>H. mabouia</i> vs. <i>H. mercatorius</i>) and species may be native	Kluge, 1969
<i>Lepidodactylus lugubris</i>	Brazil	Girard, 1858; Mechler, 1968; Auth, 1994; Rueda-Almonacid, 1999; Lever, 2003	N	Probably based on incorrect locality data	Vanzolini, 1968; Bauer et al., 2007
<i>Nactus pelagicus</i>	Pacific Islands	Lever, 2003	N	Species likely native over most or all of Pacific range	Moritz, 1987; Zug & Moon, 1995; Zug, 1998
<i>Perochirus ateles</i>	Guam	Lever, 2003	N	Native	W.C. Brown, 1976; Bauer & Henle, 1994

(continued)

Table B.1 (continued)

Species	Claimed locality of introduction	Source for claimed introduction	Valid?	Reason invalid	Evidence questioning, correcting, or providing evidence against claim for introduction
<i>Phrynosoma coronatum</i>	US: Hawaii	Jennings, 1987c	?	Unclear if "introduced" means released into wild or just imported	
<i>Podarcis dugesii</i>	Canary Islands	Museum specimens	N	Misidentified or uncertain provenance	Richter, 1998
	Madeira: Selvagen Islands	Lever, 2003	N	Native	Bischoff et al. 1989
<i>Podarcis melisellensis</i>	US: Pennsylvania	Lever, 2003, citing Kauffield, 1931	N	Mistaken identification for <i>Podarcis sicula</i> , under which it appears in Table A.1	Conant, 1959
<i>Proeopeditus lineata</i>	Mauritius	Daruty de Grandpré, 1883a, b; Koenig, 1932	N	Misidentification	Name is a mis-spelling of <i>Praeopeditus lineata</i> , an Australian skink now known as <i>Lerista praepedita</i> and certainly never introduced to Mauritius. This name was erroneously claimed by Cheke (1987) and C. Lever (2003) to be a synonym of <i>Lycodon aulicus</i> , which is established in Mauritius.
<i>Podarcis sicula</i>	Tunisia	Mertens & Wermuth, 1960; Bruekers, 2003b	?	Locality may be erroneous	Henle & Klaver, 1986
<i>Sphaerodactylus fantasticus</i>	Dominica	Evans, 1989	N	Native	R. Thomas, 1965
<i>Sphaerodactylus vincenti</i>	St. Lucia	Corke, 1987	?	Native	Schwartz & Thomas, 1965; Schwartz & Henderson, 1991
<i>Tarentola boettgeri</i>	Madeira & Selvagen Islands	Joger, 1984b	?	Uncertain where introduced	Likely introduced to one of these areas from the other but direction of movement uncertain

<i>Varanus rosenbergi</i> (syn: <i>Varanus gouldii rosenbergi</i>)	Australia: Reevesby Island	Mirtschin, 1982, 1983; Mirtschin & Jenkins, 1985; Robinson et al., 1985	?	Uncertain that not native	Schwaner, 1985
<i>Zonosaurus mada-gascariensis</i>	Seychelles: Aldabra & Curieuse	Henkel & Schmidt, 1995	?	Argued to be native	Matyot, 2003
SNAKES					
<i>Acrantophis dumerilii</i>	Réunion	Guibé, 1949, 1958; Blanc, 1972	N	Mis-assigned provenance of specimen	Bour & Moutou, 1982; Cheke, 1987
<i>Candoia bibroni</i>	American Samoa Loyalty Islands	Lever, 2003 Bauer & Sadlier, 2000; Lever, 2003	N ?	Native Probably native	McDowell, 1979; McDiarmid et al., 1999 McDowell, 1979; McDiarmid et al., 1999
<i>Dispholidus typus</i>	South Africa: Kimberly region	Siegfried, 1962	N	Native to region	Broadley, 1983; Branch, 1988; Marais, 1992
<i>Elaphe quadrivirgata</i>	Japan: Ryukyu Islands	Hikida et al., 1992; Ota et al., 1994a, 2004a; Toda & Yoshida, 2005	?	Claim derives from a folk story of uncertain reliability and island of concern lies adjacent to known native range	Nagai, 1928
<i>Helminthophis flavoterminalis</i>	Mauritius	Hahn, 1980	?	Uncertain if introduced	No evidence for claim presented; I cannot find claim repeated elsewhere in the literature
<i>Hierophis viridiflavus</i>	Spain	Falcón, 1986	N	Native	Rivera & Arribas, 1993; Lever, 2003
<i>Liophidium vailanti</i>	Reunion	Guibé, 1958; Blanc, 1972	?	If truly introduced, population no longer exists and are no available specimens to confirm identification	Bour & Moutou, 1982; Cheke, 1987
<i>Pseudonaja textilis</i>	Papua New Guinea	K.R. Slater, 1968; Menzies, 1996; O'Shea, 1996	N	Native	Kuch & Yuwono, 2002

(continued)

Table B.1 (continued)

Species	Claimed locality of introduction	Source for claimed introduction	Valid?	Reason invalid	Evidence questioning, correcting, or providing evidence against claim for introduction
<i>Ramphotyphlops braminus</i>	CNMI	W.C. Brown, 1956; Wiles et al., 1989, 1990; Lever, 2003	N	Apparently native	Pregill, 1998
<i>Typhlops lumbri-calis</i>	Guam	W.C. Brown, 1956; Lever, 2003	N	Apparently native	Pregill, 1998
TURTLES					
<i>Gopherus agassizi</i>	US: SE Arizona, SW New Mexico	D.J. Germano et al., 1994; Hulse & Middendorf, 1979	?	Uncertain if introduced or relict	Hulse & Middendorf, 1979; Patterson, 1982; Degenhardt et al., 1996
<i>Indotestudo forsterii</i>	Indonesia	Pritchard, 1979; Groombridge, 1982; Hoogmoed & Crumly, 1984; Ernst & Barbour, 1989; Iskandar, 2000	N	Native	Iverson et al., 2001
<i>Lissemys punctata</i>	Singapore	Yong, 1990; Ng et al., 1993; Iskandar, 2000	N	Misidentification	I. Das, personal communication, 1999
<i>Malaclemys terrapin</i>	Bermuda	Lever, 2003; Davenport et al., 2005	?	Native	Lever, 2003; Davenport et al., 2005; Bacon et al., 2006b; Parham et al., 2008
<i>Pelodiscus sinensis</i>	Japan: Ogasawara Islands	Ernst & Barbour, 1989; McKeown, 1996	N	Species not present in islands	M. Toda, personal communication, 2007
<i>Pseudemys floridana</i>	US: Maryland	Nemuras, 1964	N	Misidentification	Harris, 1968, 1969
<i>Testudo hermanni</i>	Mediterranean France	Fretey, 1975, 1986; Geniez & Cheylan, 1987	Y	Reintroductions or escapes in native range from which it was exterminated	Cheylan, 1984, 2001

<i>Testudo marginata</i>	France: Corsica	Honegger, 1978	N	Mis-citation of earlier work	Mertens, 1957
<i>Trachemys decorata</i>	Bahamas	D.S. Lee, 2004	N	Misreading of Seidel & Adkins, 1987	Seidel & Adkins, 1987
<i>Trachemys scripta</i>	Mexico: Baja California	Conant, 1969; R.W. Murphy, 1983; Stebbins, 1985; Ortley & Velazques-S., 1989	?	Probably native	Grismer & McGuire, 1993
	New Zealand	Lever, 2003	N	Mis-interpretation of "imported" as "released" by Lever	Robb, 1986
	US: Kentucky	Smith & Kohler, 1978	N	Mis-interpretation of cited literature	Conant, 1975; Conant & Collins, 1998
	US: Ohio	Smith & Kohler, 1978	N	Mis-interpretation of cited literature	Conant, 1975; Conant & Collins, 1998
	US: West Virginia	Smith & Kohler, 1978	N	Mis-interpretation of cited literature	Conant, 1975; Conant & Collins, 1998
CROCODILIANS					
<i>Crocodylus palustris</i>	Indonesia	Neill, 1971	?	Presence, much less introduction, of species speculative	
<i>Osteolaemus tetraspis</i>	Kenya	Lever, 2003	?	Claim or identification doubtful hearsay; no specimens; no literature citations provided	
	Madagascar	Lever, 2003	?	Claim or identification doubtful hearsay; no specimens; no literature citations provided	
MISCELLANY					
Various	Indonesia: Sulawesi	Iskandar & Tjan, 1996, Appendix B (repeated by Inger & Voris, 2001)	?	Uncertain if introduced because data and reasoned argument not presented	

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Foreign literature from languages having non-Roman scripts (Chinese, Japanese, Korean, Russian) are transliterated into Roman script. For these articles, titles translated into English are frequently provided in the original. These are used whenever provided. Otherwise, I provide a translation of the title and place it in brackets to indicate that it is not from the original publication. For many of these articles, English summaries are also provided. I make note of that when applicable; otherwise, I simply note the original language of the article. For languages using Roman script, I don't make note of the original language, presuming that will be self-evident.

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