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Have the harmful effects of introduced rats on islands been exaggerated?

David R. Towns[1,2,*], Ian A.E. Atkinson[3] & Charles H. Daugherty[2]
[1]*Terrestrial Conservation Unit, Research Development and Improvement Division, Department of Conservation, Private Bag 68-908, Newton, Auckland, New Zealand;* [2]*School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand;* [3]*Ecological Research Associates, P.O. Box 48-147, Silverstream, Upper Hutt, New Zealand; *Author for correspondence (e-mail: dtowns@doc.govt.nz; fax: +64-9-377-2919)*

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Abstract

Introduced rats are now being eradicated from many islands. Increasingly, these eradications are contested by activists claiming moral, legal, cultural, historic or scientific reasons and poorly documented evidence of effects. We reviewed the global literature on the effects of rats on island flora and fauna. We then used New Zealand as a case study because of its four-decade history of rat eradications and many detailed and innovative studies of how rats affect native species. These include use of exclosures, local manipulations of rat populations, video surveillance, and measurements of responses following eradications. The most intensive studies have been on the Pacific rat (*Rattus exulans*), a small South-East Asian species spread by Polynesians throughout the Pacific. These and the more recently introduced Norway rat (*R. norvegicus*) and ship (roof) rat (*R. rattus*) suppress some forest plants, and are associated with extinctions or declines of flightless invertebrates, ground-dwelling reptiles, land birds, and burrowing seabirds. On islands off France, Norway rats are also implicated in declines of shrews. Globally, ship rats were associated with declines or extinctions of the largest number of indigenous vertebrate species (60), including small mammals such as deer mice and bats. Effects of rats on forest trees and seabird populations are sufficiently pervasive to affect ecosystem structure and function. However, the data are patchy. Deficiencies in our knowledge would be reduced by documenting distribution and abundance of indigenous species before and after eradications. Comprehensive measurements of the responses of indigenous species to rat eradications would enable the development of testable models of rat invasion effects.

> "What a poor, curtailed, mutilated, sterile world we threaten our descendents with! Man and the rat sharing it – fit mates in many ways – in their desperate, deplorable, gnawing energy, in their ruthless destruction of every obstacle." Guthrie-Smith (1936: 218) on the lost fauna of the New Zealand subantarctic islands.

Introduction

Wherever people colonise, they spread exotic organisms, many of which become pests (e.g. Atkinson 1989). Even where permanent settlement by humans is not sustainable, introduced organisms may mark failed attempts. For example, on the subantarctic islands south of New Zealand, mice (*Mus musculus*) and rats (*Rattus norvegicus*) probably invaded with sealers and whalers; goats (*Capra hircus*), pigs (*Sus scrofa*) and rabbits (*Oryctolagus cuniculus*) were released as food for castaways; and cats (*Felis catus*), cattle (*Bos taurus*) and sheep (*Ovis aries*) either escaped or were abandoned when settlement failed (Taylor 1971; Fraser 1986). Within 100 years of the first European visit to the subantarctic islands, harvesting and introduced animals extinguished the Auckland Island merganser (*Mergus australis*). Petrels and prions, flightless teal (*Anas* spp.), snipe (*Coenocorypha aucklandica*), pipit (*Anthus novaeseelandiae*), and rail (*Rallus pectoralis*) also disappeared from the larger islands (Guthrie-Smith 1936; Fraser 1986; Towns and Broome 2003). In response to such losses, there have been calls to remove invasive species where practicable (Temple 1990; Myers et al. 2000; Donlan et al. 2003a). Increasingly, effective methods have been developed on islands around New Zealand, progressing from the removal of large herbivores such as cattle and goats to the more technically demanding eradication of rats and mice (Towns and Ballantine 1993; Mansfield and Towns 1997; Thomas and Taylor 2002; Towns and Broome 2003). Eradications of exotic animals can enable the recovery of declining native populations (e.g. Martin et al. 2000) and the re-establishment of threatened species (Myers et al. 2000). Eradication can be more environmentally sound, ethically acceptable and economically sensible than long-term pest control (Clout and Veitch 2002). However, eradications can be seen as controversial if they are considered unlikely to succeed, very expensive, cause unacceptable collateral damage (Simberloff 2002), produce adverse public reactions (Temple 1990), or have unclear benefits (Gerlach 2000).

This controversy was illustrated by some recent eradications. On 9 June 2004, helicopters began spreading 55 tonnes of brodifacoum-laced rat baits over 3000 ha Little Barrier (Hauturu) Island off north-eastern New Zealand. The aim was to kill every Pacific rat or kiore (*Rattus exulans*) which had invaded the heavily forested and rugged Nature Reserve when it was inhabited by Maori people. The immediate predicted benefits were the release of Cook's petrel (*Pterodroma cookii*) chicks from sustained predation (Imber et al. 2003), and protection of at least seven species of woody plants including the nationally threatened woodrose (*Dactylanthus taylorii*) which is at risk due to the consumption of seeds or inflorescences by rats (Ecroyd 1996; Campbell and Atkinson 2002). Also, eight adults and > 100 artificially raised juvenile tuatara (*Sphenodon punctatus*) could be released from their rodent-proof enclosure on the island. Predicted longer-term responses were increased abundance of terrestrial invertebrates such as the giant orthopteran *Deinacrida heteracantha*, recovery of many of the 13 species of resident lizards, recolonisation by small burrowing seabirds now confined to offshore rocky islets, and shifts in forest structure to produce a higher proportion of trees with fleshy fruit attractive to terrestrial birds (Campbell and Atkinson 2002; DOC 2002). Despite this compelling biological case, eradication was delayed by at least five years of argument over the cultural and historic significance of the rats (DOC 2002).

Opponents of eradications have sometimes taken direct action. In October 2001, two animal rights activists arrested on 350 ha Anacapa Island off California were accused by Federal Prosecutors of attempting to sabotage the eradication of ship (roof) rats (*Rattus rattus*). The National Parks Service believed that the rats had almost eliminated the population of the rare Xantus's murrelet (*Synthliboramphus hypoleucus*). An unrepentant activist claimed that ship rats had been demonised and that their effects on murrelets were exaggerated (Booth 2003; Kettman 2003). In May 2003, animal rights groups in the UK claimed to have halted the eradication of ship rats and Norway rats from 430 ha Lundy Island in the Bristol Channel, although the project was successfully completed (K. Varnham pers. comm.). On Lundy Island, four agencies were attempting to eradicate the rats which were implicated in significant declines of puffins (*Fratercula arctica*) and Manx shearwaters (*Puffinus puffinus*) (Appleton et al. 2002). However, the activists claimed that the toxins used were unsafe, and that ship rats were vegetarians and hence could not have consumed seabirds and were one of the rarest mammals in the UK (AA 2002).

Such objections add to controversy about eradications by raising issues of the science supporting eradications and philosophy of conservation biologists. They include claims of an inbuilt Western aversion to all rats (Roberts 1994), and that eradication programmes are driven by ecological fundamentalists quick to condemn rats (Kidson 1992) without credible evidence of any effects on the indigenous species (Donahue 2002).

Almost 2000 species of rodents are known (King in press), but few are defined as pests that directly or indirectly cause damage unacceptable to humans (Leirs 2002). In Europe, the rodent fauna of 61 species includes only five that are pests, all of which are introduced. They include house mouse, ship rat, Norway rat, musk rat (*Ondatra zibethicus*) and coypu (*Myocaster coypus*) (M. Pascal pers. comm.). Globally, four species of rodents are commonly implicated as conservation problems: house mice and three species of *Rattus*. Rats have reached about 90% of the world's islands and are among the most successful invasive mammals (Atkinson 1985; Martin et al. 2000; Donlan et al. 2003b). Removing them from islands can be expensive. For example, the Anacapa project had a budget of US$ 2 million (Davison 2003). If island eradications are based on faulty data, such expense would indeed be unjustified. Yet many reviews of the effects of invasive species conclude that cause and effect relationships between introduced rats and declining indigenous species are equivocal because of other complicating factors. Even when effects are demonstrated, their mechanisms are usually unknown (Dickman 1999; Martin et al. 2000; Courchamp et al. 2003).

We believe that there are strong ethical arguments to support eradications of introduced species such as rats when they detrimentally affect native species or ecosystems. However, claims that these effects are based on faulty evidence prompted us to examine the quality of data available. To our knowledge, no comprehensive review of rat effects has been undertaken, although there have been reviews of rat effects on birds (Atkinson 1985; Burger and Gochfeld 1994). First, we review the global literature on relationships between rat invasions and declines of indigenous species on islands. Second, we describe methods used to determine rat effects in New Zealand where the relationships between rats and indigenous species have been intensively studied for at least three decades. We also identify differences between direct and diffuse effects of rat predation, including evidence of episodic irruptions and synergistic effects between rats and other introduced species. We then use three international examples to illustrate the importance of documenting the recovery of species and ecosystems on islands after rats have been removed. We also provide three examples of controversial eradication proposals and summarise the conflict between those supporting rats and those advocating eradication. We conclude that the strong evidence of pervasive negative effects from introduced rats is sufficient to justify the high costs of eradications. We also emphasise the need to carefully measure change in systems before and after rat removal so that rat effects can be modelled for a range of native species and island systems.

Methods

Global data on rat effects

We obtained a contemporary view of rat effects by using personal contacts, Google search (rat effects on islands), and BIOSIS Advanced Search: TS = (rat AND (effect OR effects) AND (island OR islands) AND (fauna OR flora OR plant OR vegetation OR seed OR fruit OR invertebrates OR insects OR amphibians OR frog OR salamander OR reptiles OR lizard OR snake OR gecko OR skink OR bird OR seabird OR petrel OR shearwater OR tern OR predation OR predator OR extinct OR extinction)) for all document types. Reports available only as press releases and website information that could not be independently verified were then discarded. Similarly, we discarded reports of predation that did not demonstrate a population effect. We therefore confined our analysis to examples where effects such as reduced recruitment were demonstrated.

Definitions

For the purposes of this review, we group the effects of rats into four categories. Reduced or suppressed recruitment is where seeds, seedlings, eggs or juveniles are impacted sufficiently to produce population structures skewed towards adults. Suppression is where population densities are lower than would be expected, but the affected life history stage has not been identified. Catastrophic declines are where suppression of populations is so severe that there is a high probability of eventual extinction. Extinction may be of a population (local extinction) or of the species (extinction).

New Zealand case study

Demonstrating the effects of a rat invasion can be problematic. The deliberate release of rats onto previously rat-free islands might clarify these mechanisms, but the damage to island systems may be irreparable. Similarly, there are ethical and design difficulties with releasing species identified as vulnerable to rats deliberately onto islands where rats are present (Towns et al. 2003). An alternative is to study how island species respond once rats are removed (Veltman 1996), with the eradications viewed as giant experiments, even though they sometimes lack controls (Simberloff 2001).

We use the New Zealand archipelago (Figure 1) as a case study for the following reasons. First, although rat eradications elsewhere have mostly been within the last 15 years, those in New Zealand extend back at least 40 years (Towns and Broome 2003). Second, like most oceanic archipelagos, New Zealand lacks native rodents or large predatory mammals. Third, despite the absence of terrestrial mammals other than bats, New Zealand islands usually have diverse biotas enabling responses to rodents to be measured across many groups. Fourth, because the islands are frequently formed as clusters, non-treatment sites with rats and mammal-free reference sites may be present. Fifth, large subfossil deposits of native birds and reptiles have been identified and sequences of recent extinctions identified. Finally, the approximate arrival times for the two most recent commensal rat species are known. The arrival time of the third species, Pacific rat, is still hotly debated and depends on the accuracy of dates derived either from rat bones, or from deposits around species showing rat effects. Based on carbon-dated rat bones, Pacific rats were in New Zealand about 1800 years ago, 1000 years before the earliest known permanent settlement (Holdaway 1996). This would indicate early visits from people exploring the Pacific basin, or earlier settlements yet to be discovered. However, carbon dates associated with rat-affected plant and animal remains indicate the earliest effects of Pacific rats about 750 years ago, contemporaneously with the earliest known permanent Polynesian settlements (Brook 2000; Wilmshurst and Higham 2004). These inconsistencies are yet to be resolved (Atkinson and Towns in press). Regardless of date of arrival, Pacific rats were the only species of rodent in New Zealand for at least 500 years. Norway rats probably arrived during Cook's voyages of exploration, the first of which was in 1769. These two rat species co-existed on the main islands of New Zealand for at least 90 years before the arrival of ship rats, which with mice did not establish until after 1850 (Atkinson 1973; Taylor 1975). Pacific rats subsequently all but disappeared from the North and South Islands, and ship rats invaded many habitats previously occupied by Norway rats, which became confined to urban areas, farms, waterways and wetlands (Moors 1990).

By the mid-1980s, introduced rats had reached at least 142 offshore New Zealand islands ≥5 ha which, excluding Stewart Island, comprised 62% of the island combined land area (Atkinson and Taylor 1992). On some islands other introduced mammals such as cats, dogs, mustelids, Australian possums (*Trichosurus vulpecula*) and rabbits can compound rat effects. We have therefore deliberately chosen many of our examples from locations where rats are the only known introduced vertebrate.

Global examples implicating rats with species declines on islands

Our surveys of all fauna and flora added 74 reports of species affected by rats to those documented for birds by Atkinson (1985). The Biosis search located 12 reports in the primary literature where rat effects were measured outside New Zealand (Table 1).

We examined credible reports of rat effects on 173 taxa of plants and animals inhabiting 46 islands or archipelagos (Tables 1 and 2). To assess the relative impacts by rat species, 134 reports of detrimentally affected vertebrates (Figure 2) were assessed from the data reviewed here combined with a new review of seabird literature being prepared by H. Jones (pers. comm.). Most (89%) reports of the effects of Pacific rats were from New Zealand (Table 2), with the remainder for

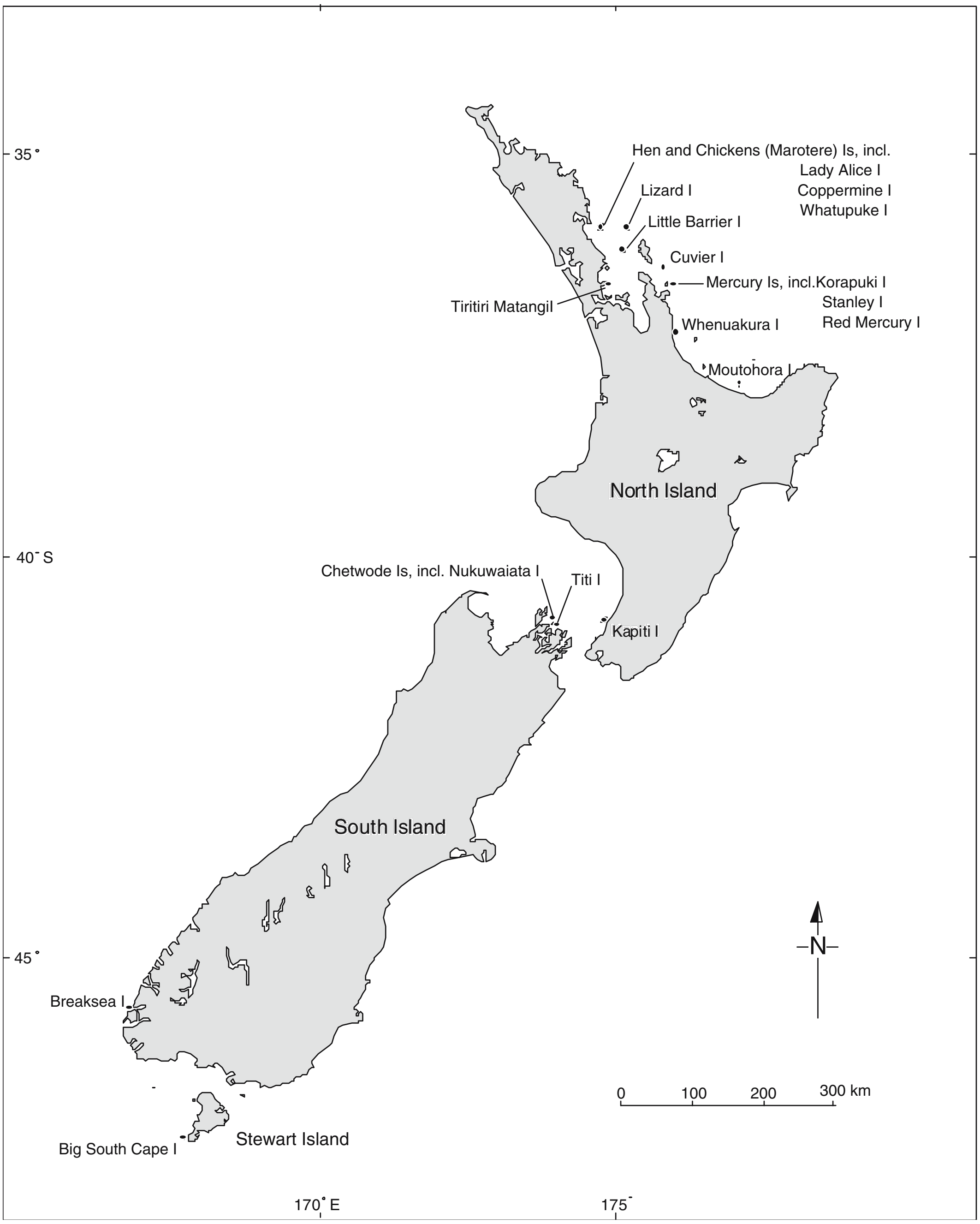

Figure 1. Localities in the New Zealand archipelago mentioned in the text.

Table 1. World list of islands separated into geographic areas where introduced rat interactions with native species are claimed, excluding seabirds reviewed elsewhere (Atkinson 1985), with *rabbits also present, **rabbits and hares also present and +cats also present.

Location	Island area (ha)	Rat species	Species affected	Evidence	References
Atlantic					
Lundy, UK	430	*Rattus norvegicus*, *R. rattus**	Manx shearwater, puffin	Anecdotal, predation of eggs and chicks	Appleton et al. (2002)
Ailsa Craig, UK	104	*R. norvegicus*	Puffin, northern fulmar *Fulmaris glacialis*, herring gull *Larus argentatus*	Post eradication fledging success	Zonfrillo (2000)
Eilean an Tighe + Gargh Eilean, Shiant Is, UK	141	*R. rattus*	Puffin	Circumstantial linkage with declines	Key et al. (1998)
Sept Iles Archipelago, France	36	*R. norvegicus*	Lesser white-toothed shrew *C. suaveolens*	Post-eradication up to 25-fold increase in shrew abundance index	Lorvelec and Pascal (in press), Pascal et al. (in press)
Tomé, France	30	*R. norvegicus*	Greater white-toothed shrew *Crocidura russula*	Post-eradication up to 17-fold increase in shrew abundance index	Lorvelec and Pascal (in press), Pascal et al. (in press)
Trielen, Molène Archipelago, France	17	*R. norvegicus*	Dunnock *Prunella modularis*, wren *Troglodytes troglodytes*, pipit *Anthus petrosus*, lesser white-toothed shrew	Post-eradication increase in numbers of breeding pairs by factors of 1.7–7 respectively, 32-fold increase in shrew abundance index	Lorvelec and Pascal (in press), Pascal et al. (in press), Kerbiriou et al. (2004)
Tenerife, Canary Islands, Spain	203,400	*R. rattus*	Shrub *Viburnum tinus*, Bolles's laurel pigeon *Columba bollii*, white-tailed laurel pigeon *C junoniae*	Heavy depletion of *V. tinus* fruit by rats leading to modified bird-plant dispersal system, reduced nesting success of pigeons revealed by artificial nests, camera surveillance	Delgado García (2000, 2002), Hernández et al. (1999)
Falkland Islands, UK		*R. norvegicus*	Cobb's wren, Blackish cinclodes *Cinclodes antarcticus*, thin-billed prion, fairy prion *P. turtur*, grey-backed storm petrel *Garrodia neries*, black-bellied storm petrel *Fregetta tropica*, Wilson's storm petrel *Oceanites oceanicus*, South Georgia diving petrel *Pelecanoides georgicus*	Comparisons between rat-inhabited and rat-free islands	D. Brown (pers. comm.), Woods (2000), Hall et al. (2002)

New Is, Falkland Islands, UK		*R. rattus*	Thin-billed prion	Observations of extensive predation	D. Brown (pers. comm.)
South Georgia Islands, UK		*R. norvegicus*	Antarctic pipit *Anthus antarcticus*, South Georgia pintail *Anas georgica*, snow petrel *Pagodroma nivea*, fairy prion, Wilson's storm petrel, South Georgia diving petrel	Comparisons between rat-inhabited and rat-free islands and mainland sites	McIntosh and Walton (2000)
Western Mediterranean					
Toro, Corsica, France	2.6	*R. rattus*	Pallid swift	80% decline following invasion by rats between 1986 and 1989	Martin et al.(2000)
Lavezzi Islands, Corsica, France	85	*R. rattus*	Cory's shearwater	Breeding success 43% without rat control, 74% after rat control, and 86% after rat eradication	M. Pascal (pers. comm.)
Balearic Islands, Spain		*R. rattus*	Local extinction of endemic tenebrionid beetles, suppression of at least 8 species of plants	Comparisons between rat-inhabited and rat-free islands	Palmer and Pons (1996, 2001)
Caribbean					
Praslin, West Indies	1.1	*R. rattus*	St Lucia whiptail lizard *Cnemidophorus vanzoi*	Post-invasion mortality	John (1999)
Great Bird, Antigua and Barbuda, West Indies	8.3	*R. rattus*	Antiguan racer, red-billed tropic bird, West Indian whistling duck	Post-eradication increase in abundance, increased nest survival	Daltry et al. (2001), Varnham (2001), K. Varnham (pers. comm.)
Sainte-Anne Islets, French West Indies	0.5–2.6	*R. rattus*	Terrestrial crab *Gecarcinus ruricola*, Audubon's shearwater *Puffinus ilherminieri*, brown noddy *Anous stolidus*, bridled tern *S. anaethetus*	Invasion in 1996–1997; post-eradication increased abundance index (crab) and breeding success (seabirds) from <5% to at least 50% in 2 years	Pascal et al. (2004), Pascal et al. (in press)
Pacific					
Anacapa, USA	350	*R. rattus*	Xantus's murrelet, deermice *Peromyscus maniculatus anacapae*	Predation of chicks and eggs, post-eradication increases in nest survival and abundance	H. Jones (pers. comm.)
San Jorge, Mexico	14 + 5 + 5	*R. rattus*	Fishing bat *Myotis vivesi*, Craveri's murrelet *Synthliboramphus craveri*	Predation of bats and local extinction of murrelets	Donlan et al. (2003b)
Oahu, Hawaii, USA		*R. rattus* (+ low proportion *R. exulans*, *R. norvegicus*)	'Elepaio	Reduced nest predation during rat control	VanderWerf and Smith (2002)

Table 1. Continued.

Location	Island area (ha)	Rat species	Species affected	Evidence	References
Rarotonga, Cook Islands		*R. exulans*, *R. rattus*+	Rarotonga flycatcher	Reduced nest predation during rat control	Robertson et al. (1994)
Fatu Hiva, Marquesas	8000	*R. rattus*	Ultramarine lorikeet *Vini ultramarina*	Declining range following spread of rats, invasion of ship rats in 2000	BirdLife International (2003)
Tasman					
Lord Howe Islands, Australia		*R. rattus*	Lord Howe Island stick insect *Dryococelus australis*	Local extinction following invasion by rats	Priddell et al. (2003)
Indian					
Boodie, Australia	170	*R. rattus*	Bettong *Bettongia lesseur*	Confined to limestone in presence of rats, post-eradication spread and up to 10-fold increase	Morris (2002)
Middle, Australia	350	*R. rattus*	Golden bandicoot *Isoodon auratus barrowensis*	Post eradication 5-fold increase in abundance	Morris (2002)
Chumbe, Tanzania	20	*R. rattus*	Roseate tern *Sterna dougalli*	Elimination of chicks by rat predation in 1994, abandonment of colony. No recolonisation despite rat eradication in 1997	C. Daniels and D. Iles (pers. comm.)
Frégate, Seychelles	219	*R. norvegicus*	Tenebrionid *Polposipes herculeanus*, Seychelles magpie-robin *Copsychus sechellarum*	Invasion in 1995 followed by declines of tenebrionds and high mortality of magpie-robin chicks, rats eradicated in 2000	Thorsen et al. (2000), Shah (2001), Merton et al. (2002)
Bird, Seychelles	101	*R. rattus*	Sooty tern *Sterna fuscata*, common noddies *Anous stolidus*, turtle doves *Streptopelia picturata*	Invasion in 1970s, widespread predation of tern eggs and chicks; rats eradicated in 1996; post-eradication shift to ground nesting by noddies, recolonisation by doves	Feare (1999), Merton et al. (2002)

Gunner's Quoin, Mauritius	65	*R. norvegicus***	Skinks *Scelotes bojerii*, *Cryptoblepharus boutonii*; night gecko *Nactus coindemirensis*	Post-eradication increases in visibility and abundance	Bell (2002)
Gabriel, Mauritius	42	*R. rattus*	Wedge-tailed shearwaters, red-tailed tropic birds	Anecdotal reports of post-eradication increases	Bell (2002)
St Paul, France	800	*R. rattus**	Macgillivray's prion *Pachyptila macgillivrayi*, grey-faced petrel *Pterodroma macroptera*	Postulated cause of decline, post-eradication recolonisation	Micol and Jouventin (2002)

seabirds on Kure Atoll in the Hawaiian archipelago (Atkinson 1985). Higher proportions were obtained outside New Zealand for Norway rats and ship rats (86 and 75% respectively). Approximately equal numbers of reptile, seabird and landbird species were affected by Pacific rats, whereas Norway rats and ship rats affected larger numbers of seabird species (Figure 2). Reported effects ranged from reduced recruitment to total extinction, with Pacific rats implicated in the total or local extinction of at least 13 species of vertebrates. However, these were all based on circumstantial evidence inferred from subfossil deposits and differences between these and contemporaneous distribution patterns. By comparison, 16/61 (26%) of species reportedly affected by ship rats were from local or total extinction after rats invaded.

These invasions provide some of the most compelling evidence of rat effects. In chronological order they include: the invasion of Lord Howe Island by ship rats when a ship grounded in 1918, following which five species (>40%) of indigenous forest birds became extinct within 5 years, and the invasion of Midway Island by ship rats in 1943, after which two species of land birds disappeared within 18 months (Atkinson 1985).

In New Zealand, the invasion of Big South Cape Island by ship rats in about 1962 was followed by the total extinction of an endemic bat and a wren. Five additional species of forest birds and one of bat became locally extinct (Table 2). The rats also killed *Pseudopanax* sp. trees by stripping foliage and bark (D. Merton pers. comm.) and chewed speargrass (species of *Aciphylla* and *Stilbocarpa*) almost to ground level. The speargrass subsequently recovered, but a large flightless weevil confined to them disappeared (Kuschel and Worthy 1996). Between 1982 and 1984, Norway rats invaded Whenuakura Island (2 ha), following which the entire population of >130 tuatara disappeared (Newman 1986). Rat effects on reptiles were also documented for Lizard Island (1 ha), which had abundant lizards, white-faced storm petrels (*Pelagodroma marina*) and little shearwaters (*Puffinus assimilis haurakiensis*). Pacific rats invaded the island in about 1977 and were eradicated within 12 months. Assessments 7 years after the

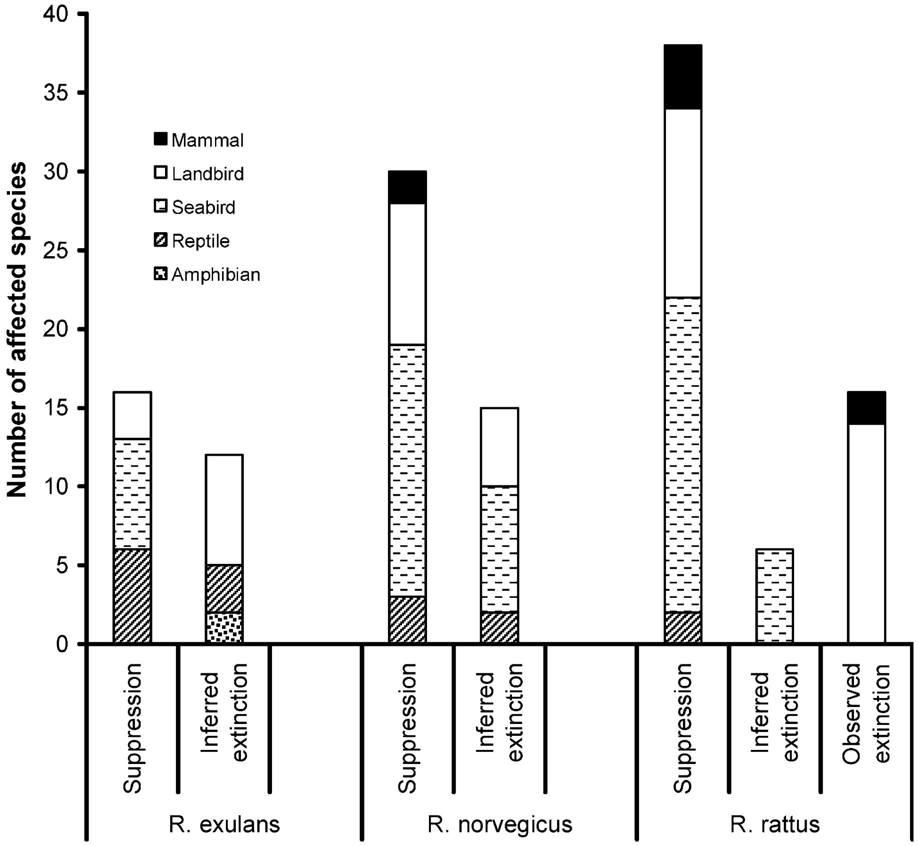

Figure 2. Credible reports of vertebrate species detrimentally affected by *Rattus exulans* ($n = 28$), *R. norvegicus* ($n = 45$), and *R. rattus* ($n = 60$), with seabird data including reports in Atkinson (1985) and assembled by H. Jones (pers. comm.). Suppression includes recruitment failure or population suppression, extinction includes local or total extinction, inferred extinction based on distributional data and observed extinction based on observed invasions.

eradication indicated no lasting effects on the seabirds, but encounter frequencies of five species of lizards still had not recovered to pre-invasion levels (McCallum 1986) (Table 2).

Other recently documented invasions include two in the Seychelles, four in the French West Indies, one in the Marquesas and one off Corsica, resulting in recorded declines of a tenebrionid beetle, terrestrial birds and seabirds. All but the Marquesas invasion were reversed by subsequent eradication of the rat populations (Table 1).

At face value, these data indicate variable effects of rats on island-inhabiting species. The fewest effects recorded were for the small Pacific rat, whereas ship rats, although smaller than Norway rats, apparently have had the most detrimental effects (Figure 2). However, recent intensive studies in New Zealand indicate far wider implications than the species-by-species effects revealed in global literature surveys.

Circumstantial evidence of rat effects in New Zealand

Studies of seed deposits, terrestrial snails, insects and small vertebrates from caves, swamps and sand dunes on the North and South Islands of New Zealand have revealed evidence of sudden exploitation and waves of local and total extinctions before 1700 AD (Holdaway 1999; Worthy and Holdaway 2002). The deposits include numerous rat-gnawed woody seeds of the trees *Elaeocarpus* spp. and *Prumnopitys ferruginea* (Wilmshurst and Higham 2004) and rat-damaged

Table 2. The effects of three species of introduced rats on the flora and fauna of New Zealand with definition of the type of evidence available using only examples where effects of other introduced mammals can be excluded and with severe effects leading to local extinction in bold.

Species affected	Locality	Mechanism	Evidence	
Rat species: Pacific rat Rattus exulans				
Climber *Ripogonum scandens*; coastal trees *Coprosma macrocarpa*, *C. repens*, *Corynocarpus laevigatus*, *Dysoxylum spectabile*, *Elaeocarpus dentatus*, *Melicytus novae-zelandiae*, *Myoporum laetum*, ***Nestegis apetala***, *N. lanceolata*, ***Pisonia brunoniana***, ***Pittosporum crassifolium***, *Pouteria costata*, *Pseudopanax lessonii*, ***Streblus banksii***; palm *Rhopalostylis sapida*; root parasite *Dactylanthus taylorii*	North-eastern and central islands	Recruitment failure and local extinction of selected species	Comparisons between rat-inhabited and rat-free islands, comparisons of seedling density between rat-proof exclosures and controls, post-eradication responses by seedlings	Atkinson (1986), Campbell and Atkinson (1999), Campbell and Atkinson (2002), Campbell (1978), Brown (1997), Aviss (1997), Eckroyd (1996), S. Ferreira (pers. comm.)
Flax snail ***Placostylus hongii***, predatory snail ***Amborhytida tarangensis***,	Lady Alice Island	Predation and local extinction	Statigraphic analyses and subfossil remains	Brook (1999)
Tenebrionid beetles ***Mimopeus* spp**.	North-eastern islands	Local extinction	Comparisons between rat-inhabited and rat-free islands	Towns et al. (1997)
Tusked weta ***Motuweta isolata***	Mercury Islands	Local extinction	Comparisons between rat-inhabited and rat-free islands	McIntyre (2001)
Ground weta *Hemiandrus* sp. and spiders *Miturga* sp.	North-eastern islands	Suppressed abundance	Post-eradication response	Green (2002)
Frogs ***Leiopelma markhami***, ***L. waitomoensis***	Northern North Island	Extinction	Extinction coincident with rat presence	Worthy (1987)
Tuatara *Sphenodon punctatus*	New Zealand	Severe range contractions, relict populations on islands	Reduced population sizes and recruitment suppression in presence of rats; recruitment pulse on rat removal	Whitaker (1978), Cree et al. (1995), Parrish, Towns and Ussher (unpubl. data)
Skink ***Cyclodina northlandi***	Northern North Island	Extinction	Extinction coincident with rat presence	Worthy and Holdaway (2002)
Skinks ***C. alani***, ***C. macgregori***	North Island	Severe range contractions, extinct on North Island, relict populations on rat-free islands	Lack of sympatry with any rat species	Whitaker (1978)
Shoreline skinks *Oligosoma suteri*, *O. smithi*; geckos *Hoplodactylus maculatus*, *H. duvaucelii*, *H. pacificus*	North Island and offshore islands	Habitat displacement to rocky shore lines	Comparisons of habitat use; direct recruitment pulse and habitat shifts on rat removal; measured decline following rat invasion	Whitaker (1978), Towns et al. (2003), McCallum (1986), Towns (1994, 2002a), Towns and Parrish (unpubl. data)
Snipe ***Coenocorypha* spp**	Offshore islands	Range contractions and local extinction	Lack of sympatry	Miskelly (1987)

Table 2. Continued.

Species affected	Locality	Mechanism	Evidence	
Owlet-nightjar *Aegotheles novaezealandiae*, **terrestrial duck** *Euryanas finschi*, **rails *Capellirallus karamu* and *Gallinula hodgenorum*, flightless and near flightless wrens *Pachyplichas yaldwini*, *Dendroscansor decurvirostris*, *Traversia lyalii***	New Zealand	Extinction with exception of *T. lyalii*, last remaining island population exterminated by cats	Declines coincident with rat presence	Holdaway (1999)
Diving petrel	Korapuki Island	Unknown	Post-eradication population expansion on rat removal	G. Taylor (pers. comm.)
Little shearwater, Pycroft's petrel	Marotere Islands	Predation of eggs and chicks	Video surveillance, post eradication fledgling survival	Booth et al. (1996), Pierce (2002)
Cook's petrel	Little Barrier Island, Codfish Island	Predation of eggs and chicks	Chick mortality and post eradication fledgling survival	Imber et al. (2003)
Saddleback *Philesternus carunculatus rufusater*	Red Mercury Island	Unknown	Post-eradication increases in encounter frequency	Robertson et al. (1993)
Rat species: Norway rat Rattus norvegicus				
Shrub *Coprosma ciliata*, climber *Ripogonum scandens*, trees *Ascarina lucida*, *Hedycarya arborea*, *Nothofagus menziesii*, *N. solandri* var. *cliffortioides*, *Pseudopanax colensoi*, *Schefflera digitata*, *Weinmannia racemosa*	Breaksea Island	Destruction of seeds and browsing of buds, flowers or seedlings	Post-eradication increases in seedling abundance	Allen et al. (1994)
Flatworms, harvestmen, spiders, isopods, hemipterans, beetles of families Carabidae, Cerambycidae (larvae), Elateridae (adults), Lucanidae (*Dorcus helmsi*), Staphylinidae (larvae)	Breaksea Sound islands	Predation	Circumstantial comparisons between rat-free and rat-inhabited islands and stomach content analyses	Bremner et al. (1984)
Tuatara	Whenuakura Island	Unknown	Local extinction following invasion	Newman (1986)
Fiordland skink *Oligosoma acrinasum*	Breaksea Island	Unknown	Not sympatric with rats on islands, recolonisation on rat removal	Thomas and Whitaker (1995)
Saddleback	Kapiti Island	Predation of chicks and eggs?	Experimental release of birds into rat population	Lovegrove (1996)
Snipe *Coenocorypha* sp.	Campbell Island	Unknown	Post-eradication recolonisation	C. Miskelly (pers comm.).
White-faced storm petrel (*Pelagodroma marina*)	Maria Island	Predation of breeding adults	Declines coincident with rat invasion, post-eradication response	D. Merton (pers. comm.)
Grey-faced petrel	Whale Island	Predation of chicks and eggs	Fledgling survival following rat removal	Imber et al. (2000)

Rat species: ship rat Rattus rattus				
Weevil *Hadramphus stilbocarpae* Saddleback *Philesternus c. carunculatus*, robin *Petroica australis*, fernbird *Bowdleria punctata*, banded rail *Rallus philippensis*	Big South Cape Island	Unknown	Local extinction following invasion	Atkinson (1989), Kuschel and Worthy (1996), D Merton (pers. comm.)
Snipe *Coenocorypha iredalei*, bush wren *Xenicus longipes*	Big South Cape Island	Unknown	Extinction following invasion	Bell (1978)
Robin, tomtit	North Island	Predation of eggs and chicks	Direct observation by photography	Brown (1997)
Yellowhead, orange-fronted parakeet	South Island *Nothofagus* forest	Unknown	Population declines and local extinction following rat irruptions	Dilks et al. (2003), Keey (2004)
Greater short-tailed bat *Mystacina robusta*, lesser short-tailed bat *M. tuberculata*	Big South Cape Island	Unknown	Last known population of greater short tailed bat disappeared after rat invasion	Daniel (1990)

shells of *Placostylus* snails (Brook 2000). On the North Island, the seed and snail-shell evidence indicated the sudden onset of damage that began about 750 years ago. On Lady Alice Island, the disappearance of *Amborhytida* snails and the appearance of deposits of rat-gnawed *Placostylus* snails in sand dunes were interpreted through radio-carbon dating to indicate an invasion about 200 years ago (Brook 1999). The only rat species present when seed damage was first recorded for the North Island, and snail damage began on Lady Alice Island, was the Pacific rat. Furthermore, cave deposits in the North and South Islands also indicate that two species of frog, a large skink, snipe, a snipe-rail, an owlet nightjar and three species of flightless or near-flightless wrens became extinct during the time Pacific rats were the only introduced vertebrate predator other than dogs (Table 2).

More specific measures of rat effects were obtained by comparing islands with and without rats. For example, the trees *Nestegis apetala*, *Pittosporum crassifolium*, *Pouteria costata* and *Streblus banksii* were rare or absent on islands with rats but a common component of vegetation on islands without rats (Atkinson 1986; Campbell and Atkinson 1999). Extensive qualitative comparisons of differences in species combinations and habitat use by lizards and tuatara showed differences depending on whether or not islands were inhabited by Pacific rats (Whitaker 1978). Similar distributional differences were recorded for large species of invertebrates (Table 2).

Direct evidence of rat effects in New Zealand

Evidence from irruptions

Episodic irruptions of rats can have effects similar to invasions. Beech (*Nothofagus* spp.) forests of the South Island of New Zealand periodically produce massive crops of seed in a phenomenon known as masting (Schauber et al. 2002). This is usually followed by increased abundances of mice and stoats (*Mustela erminea*) and sometimes of ship rats (King 1983; Dilks et al. 2003). Periodic heavy predation by stoats then leads to population crashes of hole-nesting birds such as yellowheads (*Mohoua ochrocephala*) (O'Donnell et al. 1996). In 1999 and 2000, beech produced two mast seasons in succession. Ship rats reached densities not previously encountered (Dilks et al. 2003) with disastrous consequences for yellowheads and orange-fronted parakeets (*Cyanoramphus malherbi*), which disappeared from some areas (Table 2).

Evidence from surveillance and population manipulations

Time-lapse video recording at nests of little shearwaters on Lady Alice Island revealed egg predation by Pacific rats, which were responsible for an estimated 75% of failed incubations (Booth et al. 1996). Similar methods were used to follow egg laying, incubation and chick development in 72 nests produced by North Island robin (*Petroica australis*) and North Island tomtit (*P. macrocephala*). Predation was recorded at 82% of the nests. Video photography at 27 nests documented 12 predation events, 10 by ship rats and two by the native owl *Ninox novaseelandiae*, with evidence of rat predation of chicks, eggs and at least four adult females while incubating (Brown 1997). While the small and relatively productive passerines survived some periods of intensive loss, 30% nest failure is sufficient to produce continuing declines of a New Zealand wattlebird, the North Island kokako *Callaeas cinerea wilsoni* (Innes and Hay 1995). The effects of this mortality at the population level were tested by comparing the effectiveness of predator suppression on study populations of kokako with non-treated sites. The predators most effectively controlled were possums and ship rats. Significantly more pairs of kokako fledged young in the treated areas than non-treated areas. Video surveillance indicated that possums were most likely to attack eggs, chicks and sitting females, whereas ship rats preyed on eggs in the first 10 days of incubation and occasionally on small chicks (Innes et al. 1999).

Evidence from plant recruitment studies

The effects of Pacific rats on recruitment of coastal trees were measured on Cuvier Island and Little Barrier Island. An open-topped exclosure was used on Cuvier Island and seedlings counted 2.5 and 6.5 years after rat exclusion. Numbers of seedlings of a palm and two forest tree species (Table 2) increased in the exclosure relative to adjacent control areas (Campbell 1978). On Little Barrier Island, seeds of species inhibited on Cuvier Island and showing recruitment depression on rat-inhabited islands, were added to Pacific rat-proof exclosures and to control areas accessible to the rats. By comparing plant size classes on rat-inhabited and rat-free islands, measuring the responses after rat eradication and the response of seeds in exclosures, recruitment depression by Pacific rats was shown for 11 species of forest plants (Campbell and Atkinson 2002). Three additional species were too rare for use in exclosures, but their disjunct distribution and lack of regeneration on rat-inhabited islands indicates inhibition by rats (Table 2).

Evidence from rat removal

The vulnerability of at least three species of plants was confirmed by significant increases in seedling abundance after Pacific rats were eradicated from Nukuwaiata Island (Brown 1997; Aviss 1997). Responses of plants to the eradication of Pacific rats appear to reflect the combined effects of vulnerability of seeds and seedlings and the plants' reproductive output. For example, *Pisonia brunoniana* is an uncommon tree on Pacific rat-inhabited Hen Island, but on nearby Lady Alice Island seedlings became abundant under mature trees after eradication of Pacific rats. *Streblus banksii* appears to have been similarly affected by Pacific rats on both islands, but seedlings are still rare on Lady Alice Island. This may be because the species is dioecious and many of the remaining trees are widely separated (D.J. Campbell pers. comm.).

Possible effects of Norway rats on forest plants were studied on Breaksea Island. Allen et al. (1994) found a recruitment lapse in two species of southern beech (*Nothofagus* spp.) beginning about 100 years ago and coincident with the probable time of Norway rat establishment. Seedlings of *Nothofagus* counted at the time of rat eradication in 1988, and over the following five years, increased in abundance after rat-removal suggesting previous seed consumption. Overall, nine species of trees and shrubs showed higher seedling numbers after rat removal compared with the year rats were removed, and six of these had fleshy fruits (Table 2). Three species with small seeds showed similar increases, probably due to release from browsing of buds, flowers and seedlings. Recruitment of at least five species declined after rat removal, probably reflecting a recovery of herbivorous invertebrates also vulnerable to rat predation (Allen et al. 1994).

Invertebrate responses to rat eradications have not been well documented. Following removal of Pacific rats from Korapuki Island, flightless and poorly dispersed species recorded for the first time were three species of cockroaches, one of tenebrionid beetle, two of carabid beetle, a coastal dermapteran, a flightless orthopteran (Rhaphidophoridae), isopods and a species of large centipede (Green cited in Towns et al. 1997). These rapid changes were apparently independent of vegetation changes later recorded in response to rabbit removal. Increased captures of flightless orthopterans (Anostostomatidae) and large prowling spiders (Miturgidae) in pitfall traps were also reported after the removal of Pacific rats from Tiritiri Matangi Island (Green 2002).

Some lizard species rapidly responded on northern islands following rat removal. On Korapuki Island, capture rates of diurnal shoreline inhabiting skinks *Oligosoma smithi* increased up to 30-fold after removal of Pacific rats (Towns 1994). Similar increases were recorded for shoreline populations of common geckos (*Hoplodactylus maculatus*), which were extremely rare before rats were removed. After 15 years without rats, sighting frequencies increased 28-fold and were equal to those on a neighbouring rat-free island (Towns 2002a). The nocturnal shoreline skink *Oligosoma suteri* on Coppermine Island was also more frequently captured after the removal of Pacific rats than while rats were present, but *O. smithi* in the same habitat showed no significant change over the same 2.5 years (Towns et al. 2003). Another diurnal shoreline species, *O. acrinasum*, was never seen on islands inhabited by Norway rats, but naturally recolonised Breaksea Island from offshore rocky outcrops once the rats were eradicated (Thomas and Whitaker 1995).

Seabirds can show variable responses to rats. Pierce (2002) found increased fledging success of little shearwaters and Pycroft's petrels (*Pterodroma pycrofti*) on Lady Alice and Coppermine Islands when Pacific rats were removed, but the extent of change varied between the two islands. Species such as diving petrels (*Pelecanoides urinatrix*) were predicted to be vulnerable to rats because of their small size (130 g) and winter-nesting habits (Imber 1978; Holdaway 1999). This appears to be supported on Korapuki Island, where two highly constrained populations present before Pacific rats were removed in 1986 (Hicks et al. 1975) had by 2003 expanded to include much of the coastline occupied by at least 1000 pairs (G. Taylor pers comm.). However, there was no measurable change in the abundance of the much larger (560 g) grey-faced petrels (*Pterodroma macroptera gouldi*) 10 years after the removal of Pacific rats from Stanley Island (G. Taylor pers comm.). Similarly, there was no measurable change in the abundance of the 850 g sooty shearwaters (*Puffinus griseus*) or the 700 g flesh-footed shearwaters (*P. carneipes*) over a 12-year sample period that began about 10 years after the removal of Norway rats from Titi Island (Gaze 2000).

Species-specific effects of rats on forest birds were found on Kapiti Island, where Pacific rats and Norway rats co-existed. Nests of forest parrots *Nestor meridionalis* > 1 m above ground level were not affected by Pacific rats but 50% of nests within one metre of the ground, and therefore accessible to Norway rats, were destroyed (Moorhouse 1990). Translocations of saddlebacks to Kapiti Island were failing before rats were eradicated even though the birds had been successfully translocated to seven islands inhabited by Pacific rats but not Norway rats (Lovegrove 1996). Saddlebacks rapidly increased on Kapiti Island after both species of rats were eradicated (Miskelly and Robertson 2002).

Responses to rat removals by terrestrial birds are often complicated by the previous presence of multiple predator species, other management activities, or even forest succession, so that the effects of individual rat species are difficult to separate. For example, on Tiritiri Matangi Island increases in the encounter rates of bellbirds (*Anthornis melanura*), red-crowned parakeets

(*Cyanoramphus novaezelandiae*) and saddlebacks (*Philesturnus carunculatus*) were recorded after the eradication of Pacific rats. However, active forest planting, and successional change of the young forest over the sample period may have influenced the response (Graham and Veitch 2002). Nonetheless, Robertson et al. (1993) also reported increased encounter rates of saddlebacks on Red Mercury Island after removal of Pacific rats and in the absence of forest manipulation.

Synergistic and indirect effects of rats in New Zealand

On Moutohora (Whale) Island, 30,000–40,000 grey-faced petrels co-existed with Norway rats, and 29–47% of the breeding pairs successfully reared a fledgling during 1968–1971 (Imber et al. 2000). Rabbits introduced to the island in about 1968 rapidly increased to reach an estimated 375/ha by 1973, at which point virtually no petrels were fledged due to heavy predation by rats. Up to 30,000 chicks were lost each year until rats were controlled and finally eradicated in 1987. The accelerated predation by rats was attributed by Imber et al. (2000) to the exploding population of rabbits that then provided rats with alternative food in the form of young and dead rabbits. This phenomenon was independently modelled by Courchamp et al. (2000) using interactions between rabbits and cats to explain the extinction of parakeets from Macquarie Island (Taylor 1979). Courchamp et al. (2000) predicted that hyperpredation can result from predator populations suddenly able to increase through the introduction of alternative and prolific prey. A similar effect was postulated by Moller and Craig (1987) for Pacific rats living at high densities in grassland. They predicted that when grass seed production collapsed annually at the end of summer the dense populations of Pacific rats would have particularly severe effects on non-preferred prey.

Given the wide range of effects attributed to commensal rats, it seems likely that indirect effects would follow their invasion of new locations. For example, Towns (2002a) found a negative relationship on islands between the presence of Pacific rats and distribution of the honeydew scale insect *Coelostomidia zealandica*. The scale, which has flightless females, infests the coastal trees *Pittosporum crassifolium* and *Myoporum laetum*. However, *P. crassifolium* can be largely eliminated from islands invaded by Pacific rats (and probably other rat species) (Atkinson 1986). On the Marotere Islands inhabited by Pacific rats, *P. crassifolium* is rare and the scale cannot be found, yet *P. crassifolium* and scale are abundant on small islets offshore without rats. This absence has wider implications because the scale insects produce exudates used as high-energy food by geckos and honey-eating birds.

Circumstantial relationships confirmed by eradications

Confirming global rat effects

Previously published reviews relied on observations of mortality or sudden declines after invasions to demonstrate detrimental effects of rats on birds. These include at least 25 genera of seabirds in 9 families detrimentally affected by rats (Atkinson 1985; H. Jones pers. comm.). Local or total extinction may seem unequivocal, but we found one report where a tern supposedly affected by rats may have only intermittently used the breeding area before the invasion. For vertebrates, we found 28 studies of 45 species (29 birds) where the effects of invasions were quantified, or where predictions about rat effects were tested by manipulating rat population density or observing the responses to rat eradication. In an innovative study of rat effects on islands off Corsica, Penloup et al. (1997) measured declines of pallid swifts (*Apus pallidus*) after a ship rat invasion, compared nesting success on rat invaded and rat free islands, and used photography of predation at artificial nests to measure site effects. The following examples are of circumstantial relationships confirmed by eradications for a range of species and locations.

Tuatara – Pacific rat interactions in New Zealand

Reduced recruitment of juvenile tuatara on islands with Pacific rats compared with those lacking rats was first proposed by Crook (1973).

Cree et al. (1995) surveyed 11 islands, and also found recruitment failure and low encounter rates of tuatara on islands with Pacific rats. Of 12 islands where Pacific rats and tuatara co-existed over the last 150 years, tuatara were extinct on four, and showed evidence of recruitment failure and low encounter rates on seven. Only the Lady Alice Island population showed evidence of juvenile recruitment. Cree et al. (1995) proposed that Pacific rats affected tuatara through competition for food and predation on eggs and juveniles.

Dietary studies of Pacific rats co-existing with tuatara failed to confirm direct detrimental effects, with no evidence of regular intake of tuatara by rats. For example, on Lady Alice Island 134 rat stomachs examined by Newman and McFadden (1990) contained no tuatara remains. Likewise, G. Ussher (pers. comm.) found no tuatara remains in 160 Pacific rat stomachs in 1993 on Lady Alice Island and neighbouring Whatupuke Island. A dietary overlap between Pacific rats and tuatara identified by Cree et al. (1995) was confirmed by Ussher (1999). No negative effects of this overlap were identified since tuatara had body weights apparently unaffected by the presence of Pacific rats (Cree et al. 1995). Furthermore, Tyrrell et al. (2000) found no relationship between gravidity rates, clutch size and body size of female tuatara and the presence of Pacific rats. Instead, gravidity on Lady Alice Island 3–4 years after Pacific rats were removed was within the range observed by Newman et al. (1994) when the rats were present. Tyrrell et al. (2000) therefore predicted that continued suppression of tuatara recruitment in the presence of Pacific rats was through predation of eggs and young, although this was supported by just one likely predation of a young tuatara (Newman 1988). However, when Pacific rats were removed from Lady Alice Island, the proportion of immature tuatara of snout–vent length < 180 mm increased from 2.4% in the presence of the rats to 43% eight years after the rats were removed (R. Parrish, D. Towns and G. Ussher unpublished data). Such high proportions of juveniles were never previously reported on Lady Alice Island, nor on any other islands inhabited by Pacific rats. Similar results were subsequently obtained on two neighbouring islands (R. Parrish and G. Ussher pers. comm.).

Antiguan racer–ship rat interactions in the West Indies

The Antiguan racer (*Alsophis antiguae*) is a colubrid snake that once inhabited the Lesser Antillian archipelago and the neighbouring island of Barbuda, but largely disappeared following the introduction of the Asian mongoose (*Herpestes javanicus*). The racers were regarded as extinct until their rediscovery on 9.9 ha Great Bird Island in the early 1960s. However, ship rats had reached this island and more than 50% of the remaining 51 racers showed scarring consistent with rat bites (Daltry et al. 2001). Eight years after rats were eradicated from Great Bird Island in 1995, the racer population had at least doubled, scarring from bites was reduced to 5% and became confined to large, old individuals (Daltry et al. 2003). Ship rats have subsequently been eradicated from 12 additional islands and the racers re-introduced to two of them. As a by-product of these eradications, vegetation biomass and diversity increased (Daltry et al. 2001), red-billed tropic birds (*Phaeton aetherecus*) doubled in number (Ross 2000), and reproductive output of West Indian whistling ducks (*Dendrocygna arborea*) also increased (Daltry et al. 2001).

Cobb's wren–Norway rat interactions in the Falkland Islands

The Falklands archipelago comprises about 700 islands, 90 of which have been invaded by rats (D. Brown pers. comm.). Surveys of 59 islands showed ground-nesting Cobb's wren (*Trogolodytes cobbi*) confined to 23 islands unoccupied by Norway rats (Hall et al. 2002), whereas foliage nesting grass wrens (*Cistothorus platensis*) were present on 21 islands occupied by rats (Woods 2000, R. Woods pers. comm.). Distributions analogous to that of Cobb's wren were also found for six species of seabirds (Table 1). The likely relationship between these distributions and the effects of Norway rats was supported by local observations of almost total destruction of previously widespread thin-billed prion (*Pachyptila belcheri*) colonies on Bleaker Island after Norway rats invaded in the 1960s (D. Brown pers comm.). Rats were eradicated from two islands in 2001 (Brown et al. *2001*), and Cobb's wren were reported on both by early 2004, although breeding is yet to be confirmed (R. Woods pers. comm.).

Discussion

The politics of eradications

Any proposal to eradicate or even control invasive species can be controversial. For example, critics of attempts at curbing the spread of native plants raised accusations of nativism, racism and xenophobia, while ignoring the ecological and economic impact of the exotic invaders (Simberloff 2003). Proposals to eradicate or control rats have produced similar debate, including arguments in the scientific community over the cultural or historical significance of introduced species (Table 3). Despite at least 40 successful rat eradications in New Zealand (Towns and Broome 2003), the eradication of Pacific rats from Little Barrier Island was hotly contested (Rudman 2003). For example, some argued that Pacific rats were a cultural and historic resource deserving their own island sanctuaries (Roberts 1994; Craig 2002), whereas others countered that the case against these rats was so clear, that delaying their eradication was irresponsible and unethical (Gibbs 1999; Clout 2003). One of the most widely used accusations is that there is no credible evidence of detrimental effects by rats on native plants or animals (e.g. Craig 1986; Table 3). Such evidence is virtually impossible to obtain at locations where rats have already eradicated native species or reduced them to critically low numbers, which was one of the arguments used against the ship rats on Anacapa Island (Table 3). On the other hand, we have identified numerous ways in which rat effects have been measured (Tables 1 and 2) despite the difficulties of working at the scale of whole islands. The need for these data should not be seen as an excuse for inaction. Sometimes it may be necessary to trade off between long and complicated processes of public consultation that may never satisfy everyone and the loss of critically threatened populations or species. For example, had current technology been available in 1962, swift action might have stemmed the invasion of ship rats on Big South Cape Island before a species of wren and of bat were extirpated. However, even with technology available, eradication of Pacific rats from Little Barrier Island was delayed by prolonged consultation until likely collapse of the Cook's petrel population (Imber et al. 2003) made swift action essential.

In the end, weighing arguments of moral, legal, cultural and historic significance of an invasive species against its ecological or economic impacts may require value judgements outside the domain of science (Lawton 1997). Science can inform value judgements; for example, by modelling the effects of introduced rats on indigenous species. For these models to be useful, they need support from robust data.

Methods of obtaining robust data

Beyond anecdotal reports of species declines after invasions, rat effects have been assessed from studies of rat diet, distributional comparisons of rats and their prey through time and space, rat-proof exclosures, localised reductions of rat populations, video surveillance and responses by resident species after rats are removed. Some of these methods can, however, produce misleading results if interpreted at face value. For example, studies of Pacific rat diet in New Zealand revealed no predation or even scavenging of tuatara, which contradicted evidence of negative impacts from distributional and demographic comparisons (Newman and McFadden 1990; Cree et al. 1995). Similar results were obtained when assessing the effects of ship rats on seabirds in the Shiant Islands off Scotland. Estimates of population density (McDonald et al. 1997) and a short-term study of movements and faecal contents of the rats (Key et al. 1998) indicated little evidence of predation on chicks and eggs, so rat control was judged unnecessary. However, subsequent comparisons of stable carbon and nitrogen isotope signatures with those of likely rat prey indicated a greater role of active predation of seabirds by ship rats than had been previously apparent (Stapp 2002). The great danger with dietary studies is that they are a good indicator of recent meals but a poor indicator of impacts on populations, particularly when the prey is

Table 3. Examples of controversial rat eradication or control proposals, including arguments in principle (general) and those site-specific (specific).

Species	Location	Arguments against proposed action	Arguments in support of proposed action
Pacific rat	Little Barrier Island Nature Reserve, New Zealand (eradication commenced: 2004)	*General*: Loss of scientific data for morphological analysis and genetic data on centres of Pacific origin; lack of consultation with Maori; loss of traditional ecological and cultural knowledge (Roberts 1994); labelling as pest reflecting Western atavistic loathing for rats (Roberts 1994; Lee 2002); cultural treasure protected by Treaty of Waitangi between Crown and Maori; should be viewed as indigenous (Donahue 2002); traditionally understood as vegetarian living harmoniously with environment and with little effect on other species (Haami 1994). *Specific*: Use of toxins culturally offensive to Maori; biodiversity protection could be achieved by harvesting rats; effects supported by dubious science (Donahue 2002); loss of historical links; lack of reasoned debate (Craig 2002); insufficient consultation or resources for Maori (Kapa 2003)	*General*: Legislation defining nature reserves requires removal of exotic species where practicable (Donahue 2002; Kapa 2003). *Specific*: Need to arrest loss or declines of forest plants, burrowing seabirds, tuatara, lizards, invertebrates (Clout 2003); decline and potential extinction of giant orthopteran (Gibbs 1999); imminent crash of largest endemic Cook's petrel population (Imber et al. 2003); would enable recolonisation by other seabird species (DOC 2002); recovery of tuatara (Gaze 2001); harvesting of rats ineffective, risky (Clout 2003); control a temporary solution, not financially viable, would not enable ecosystem recovery (DOC 2002); project delayed and debated for 13 years (Rudman 2003)
Ship rat	Anacapa Island, Channel Islands National Park, California, USA (eradication completed: 2001)	*General*: Exotic species become integrated into new ecosystems (Kettmann 2003); rats have been demonized; park managers have rodent phobia; island restoration is a jihad against non-native species (Sappenfield 2002; Booth 2003); judgements by biologists are moral, not scientific; killing animals is unethical (Kettmann 2003). *Specific*: no evidence of detrimental effects on seabirds; toxins to be used inhumane (Booth 2003; Kettmann 2003)	*Specific*: Significant recovery of Xantus's murrelets; probable recovery of Ashy storm petrel (*Oceanodroma homochroa*), Cassin's auklets (*Ptychoramphus aleuticus*) (McChesney and Tershy 1998), many species of terrestrial and migratory birds, plants, (including trees such as oaks), terrestrial and marine invertebrates, salamanders and lizards (Anon 2000; NPS 2003) and potentially, endemic deermice (Pergams et al. 2000; NPS 2003)

Table 3. Continued.

Species	Location	Arguments against proposed action	Arguments in support of proposed action
Ship rat	Shiant Islands, Scotland, UK (no management undertaken to date)	*General*: An endangered species in the UK (McDonald et al. 1997: Flowerdew 2004); literature indicates mainly herbivorous (McDonald et al. 1997) and any predation of seabirds less intense than Norway rats (Key et al. 1998); does not prey on other species; seabird declines may be due to over fishing of sand eels; top-table conservation groups attempting to restore ecological harmony through wholesale slaughter; rats less common than seabirds [in UK] (AA 2002). *Specific*: Only UK location with ship rats isolated from other rat species; at limits of range in Eurasia; diet studies show little evidence of predation on the more abundant seabirds (McDonald et al. 1997); unique ecological resource of scientific interest (Key et al. 1998)	*Specific*: Potential threat to at least six species of sea birds (Stapp 2002); specific threat to storm petrel *Hydrobates pelagicus* (McDonald et al. 1997; Stapp 2002); comparisons of rat diet and isotope signatures indicate marine component previously underestimated; carbon isotopes consistent with consumption of seabird eggs and chicks (Stapp 2002)

rare or affected intermittently. In such examples, sensible conclusions can only be reached by using several sources of corroborating evidence. Stapp (2002) proposed that such evidence should be obtained in the Shiant Islands from studies of nest predation and egg and fledgling survival.

Apparently compelling examples of the effects of invading rats are provided by subfossil deposits that show species extinctions and declines. However, such temporal relationships can lead to conceptual blind alleys. It is not possible to prove from deposits that the disappearance of an indigenous species was caused by the appearance of its alleged predator. Widely divergent conclusions have been drawn from such data. For example, declines and extinctions of large invertebrates and small vertebrates in New Zealand are often attributed to the direct effects of predation by Pacific rats (e.g. Worthy and Holdaway 2002). Using similar evidence, Athens et al. (2002) argued that predation of birds by Pacific rats was rare, and attributed extinctions of lowland forest birds in Hawaii to the indirect effects of rats causing extensive forest modification. Our review provides evidence of direct *and* indirect effects.

Comparisons between the biotas of rat-inhabited and rat-free islands have frequently been used to develop models of rat effects. Large data sets have been used to define such relationships for beetles on 51 Balearic islands in the Mediterranean (Palmer and Pons 1996), terrestrial reptiles on 63 islands around north-eastern New Zealand (Whitaker 1978), land birds on 59 Falkland islands (Hall et al. 2002) and colonial birds on 72 islands in the western Mediterranean (Martin et al. 2000). These consistently showed lower diversity of indigenous species in the presence of rats, especially on the smaller islands. However, Caughley and Gunn (1996) warned that these circumstantial comparisons are insufficient to demonstrate cause and effect, suggesting instead that they should be used to develop testable hypotheses.

Such hypotheses are now being tested. Experimental rat control arrested declines of flycatchers (*Pomarea dimidiata*) in Rarotonga (Robertson et al. 1994; Robertson and Saul 2004), elepiao (*Chasiempis sandwichensis*) an endemic flycatcher in Hawai'i (VanDerWerf and Smith 2002), white-chinned petrels (*Procellaria aequinoctialis*) on islands in the Crozet Archipelago (Jouventin et al. 2003) and Cory's shearwaters (*Calonectris diomedea*) on islands off Corsica (M. Pascal pers comm.). Not surprisingly, eradications of rats have produced similar results. In New Zealand, predictions of Pacific rat effects on tuatara and lizard recruitment were supported once the rats were eradicated. In the Caribbean, similar responses were obtained for the Antiguan racer, and in the Mediterranean for Cory's shearwater (Lorvelec and Pascal in press). The eradications have sometimes been replicated, for example adding strength to inferences for the effects of Norway rats on shrews on islands off Brittany (Pascal et al. in press). Even more revealing have been unpredicted responses to eradications. In addition to predicted improved breeding success for a species of noddy and shearwater (Lorvelec and Pascal in press), the eradication of ship rats from Hardy Island, Martinique, was followed by unpredicted increases of terrestrial crabs. Likewise, the eradication of ship rats from Antiguan islands provided unexpected benefits for whistling ducks and surface-nesting seabirds (Daltry et al. 2001), and eradications of Norway rats from islands off Brittany unexpectedly benefited two species of shrews (Pascal et al. in press).

Even where hypotheses have been tested, cause-and-effect relationships may still prove elusive. For example, although recruitment of young tuatara into populations greatly increased after eradication of Pacific rats from New Zealand islands, how the rats reduced recruitment still remains unclear. Mechanisms for the negative relationships between native shrews and Norway rats are also unknown (M. Pascal pers. comm.). Establishing such mechanisms may often be an unreachable goal. Given the complexities of historic change and the problems of designing replicated experiments, simply demonstrating that rats have an effect can be a significant task on its own. Furthermore, testing hypotheses by measuring how systems respond to removal of rats (Veltman 1996) can only record responses from species that survived *with* rats (Towns et al. 2003) unless locally extirpated species can naturally recolonise.

Models of rat effects on terrestrial systems

One of the most intensively studied rat species is the Pacific rat in New Zealand. By use of exclosures and measuring post-eradication responses, Pacific rats have been shown to suppress coastal and lowland plants, flightless orthopterans, beetles, tuatara, geckos, shoreline skinks and some forest birds. Video surveillance has also demonstrated predation of eggs of small seabirds, the effects of which have been confirmed by studies of chick survival before and after Pacific rat eradications (Table 2).

The above studies add credibility to models of likely prehistoric effects of Pacific rats on the New Zealand mainland based on evidence from seed, bone and shell deposits. The effects may appear selective (Table 4), but there can be ecosystem-level consequences. They include: plants so heavily suppressed by Pacific rats that successional pathways and forest structure have been modified (Campbell and Atkinson 1999, 2002); and small seabirds such as diving petrels suppressed to levels that could influence nutrient-rich island environments. These plant and seabird effects have food-chain implications for many other components of island systems (Mulder and Keall 2001; Markwell and Daugherty 2002, 2003; Towns and Atkinson 2004), but the ecosystem effects of Pacific rat invasions have yet to be studied.

The effects measured for Pacific rats are likely to be exceeded by the larger rat species. Our review supports earlier predictions for birds (e.g. Atkinson 1985). The range of vertebrate species affected by rats varies, with Pacific rats being the least damaging and ship rats the most. Ship rats have recorded effects on the widest range of species, are associated with the largest number of extinctions and are the only species implicated in declines of endemic marsupials and extinctions of bats and rodents (Table 4).

Our summary suffers significant gaps. For example, very little is known about the effects of Pacific rats outside New Zealand. Within New Zealand, there have been few studies of the effects of the three rat species within the same biogeographic areas. Despite inaccurate claims that ship rats are 'vegetarian' (AA 2002), we only located studies in the Balearic and Canary Islands that investigated the effects of ship rats

Table 4. Summary of the effects of three species of introduced rats on island flora and fauna, using only observations of significant mortality, measured declines, responses to rat manipulations or credible circumstantial evidence, from data reviewed here and with rat behavioural data from Atkinson and Towns (in press), Moors (1990), and Innes (1990) (respectively), additional references to birds from Atkinson (1985) and bats from Daniel and Williams (1984). Regional abbreviations for islands: Caribbean (Car); Indian Ocean (Ind); Mediterranean (Med); North Atlantic (NAtc); North Pacific (NPac); South Atlantic (SAtc); South Indian Ocean (SIn); South Pacific (SPac).

Species and habits	Circumstantial in space or time	Direct observation or manipulation
Pacific rat: Reluctant swimmer < 50 m; largely terrestrial (will climb); 70–120 g	Invertebrates: local extinction large land snails, large flightless orthopterans and beetles (SPac) Amphibians: extinction 2 species frogs (SPac) Reptiles: extinction/local extinction 3 species nocturnal forest skinks (SPac) Birds: extinction owlet-nightjar, terrestrial duck, rails, wrens; local extinction snipe, flightless wren (SPac)	Plants: reduced recruitment 11 species forest trees, one species of palm and one of climber; catastrophic declines 4 additional tree species (SPac) Invertebrates: reduced recruitment some spiders, small flightless orthopterans and beetles (SPac) Reptiles: catastrophic declines tuatara; reduced recruitment 2 species shoreline skinks, 3 species geckos (SPac) Birds: reduced recruitment burrowing seabirds (SPac); petrels, tropic birds, grey-backed tern *Sterna lunata* (NPac); and forest birds including saddleback, robin (SPac)
Norway rat: Strong swimmer > 600 m; largely terrestrial; 350–450 g	Invertebrates: suppression tenebrionid beetles (Ind); suppression of flatworms, harvestmen, spiders, isopods, hemipterans and carabid, cerambycid, elaterid, lucanid and staphylinid beetles (SPac) Birds: local extinction wrens, cinclodes (SAtc)	Plants: reduced recruitment 7 species forest trees, one species of shrub and one of climber (SPac) Reptiles: local extinction tuatara, one species of shoreline skink (SPac); suppression skinks, night geckos (Ind) Birds: Local extinction forest birds (saddleback), snipe (SPac); suppression pipits (NAtc, SAtc); dunnock (NAtc); magpie robin; wrens (Ind); song sparrow *Melospiza melodia*, peregrine falcon *Falco peregrinus* (NPac); banded rail *Rallus philippensis* (SPac); avocet *Recurvirostra avosetta* (NAtc); pintail (SAtc); reduced recruitment burrowing seabirds < 750 g (SPac); puffin, northern fulmar, gulls (NAtc); murrelet (NPac); cahow *Pterodroma cahow* (Car); sooty tern *Sterna fuscata* (SIn); least tern *S. albifrons*, roseate tern, common tern *S. hirundo*, Arctic tern *S. paradisea*; sandwich tern *S. sandvicensis* (NAtc); common noddy *Anous stolidus* (Car) ; local extinction prions, snow petrel, diving petrels (SAtc); storm petrels (SAtc, SPac) Mammals: Suppression white-toothed shrews (NAtc)

Ship rat: Capable swimmer 300–750 m; terrestrial and arboreal 100–180 g	Invertebrates: tenebrionid beetles (Med)	Plants: suppression of at least 8 species forest trees (NAtc)
		Invertebrates: local extinction large flightless weevil; stick insect (SPac)
		Reptiles: suppression teiid lizard, colubrid snake (Car)
		Birds: extinction snipe, wren; reduced recruitment and local extinction forest birds including parakeets, fernbird, rail, wattlebirds, honeyeaters (SPac); flycatchers (SPac, NPac); swift (Med); turtle dove (Ind); pigeons (NAtc); canary *Serinus canaria* (NPac); whistling duck (Car); extinction Laysan rail *Porzana palmeri* (NPac); Lord Howe Island warbler *Gerygone insularis*, Lord Howe fantail *Rhipidura cervina*, robust silvereye *Zosterops strenua*, Lord Howe starling *Aplonis fuscus hullianus* (SPac); Laysan finchbill *Telespyza cantans*, (NPac); reduced recruitment and local extinction burrowing seabirds < 260 gm (SPac); shearwaters (Med, Ind, Car); puffin, auklets, murrelets (NPac); terns, noddies, tropic bird (Ind, Car); petrels, prions (SIn, SAtc); storm petrels (NPac, Med); Kerguelen petrel *Pterodroma brevirostris* (SIn); Bonin petrel *P. hypolueca*, dark-rumped petrel *P. phaecopygia sandwichensis* (NPac)
		Mammals: suppression of marsupials including bettong, bandicoot (Ind); suppression of fishing bat, deermouse (NPac); extinction three species bats (SPac); two species *Rattus* (Ind), two species cricetine rodents (NPac)

on indigenous plants. Furthermore, New Zealand studies indicate that the impacts of rats can vary by location, season and year (e.g. Imber et al. 2003). Massive predation of animals can result from periodic flushes of palatable seeds and fruit but may also stem from synergistic effects when other introduced organisms are used by rats as an additional food source. In these circumstances cause-and-effect relationships may be difficult to identify without long-term studies. Nonetheless, our review provides little support for claims that the effects of introduced rats have been exaggerated. On the contrary, a growing literature points to pervasive effects, despite the examples available being patchy, geographically scattered and biased towards a narrow range of more easily studied vertebrates. The first comprehensive studies of the effects of rats on forest vegetation (e.g. Campbell and Atkinson 2002) now provide worrying evidence that the effects of introduced rats on islands probably have been greatly underestimated.

In theory, improved field studies should produce better data and reduce the conflict between agencies attempting to control or eradicate rats and organisations or individuals advocating for the rats. In practice, improving data quality raises a dilemma. Some of the most convincing evidence of rat effects comes from measuring the response by species and assemblages when rats are removed, which is the very approach that advocates for rats oppose. This dilemma may originate from conservation biologists. Despite numerous completed eradications of rodents, especially in New Zealand, there are few publications in the primary literature that describe the benefits (Simberloff 2001). This is understandable in view of the daunting task of measuring change at the ecosystem level (Donlan et al. 2003a), especially when some very long-lived species may take decades to respond (Towns 2002b). The task may be made less daunting, and fitted to realistic time scales, by targeting response measures to those groups of organisms that demonstrate global vulnerability to rats. These are likely to include the following species or guilds:

1. *Vulnerable to the three species of commensal rats*: plants with fleshy fruit and/or fruit with large edible seeds (Allen et al. 1994; Campbell and Atkinson 2002), or with heavily scented inflorescences (Eckroyd 1996), or dioecious reproductive systems (Campbell and Atkinson 2002), or reliant on seabird effects such as enriched soil or open disturbed ground (not yet demonstrated for ship rats) (Norton et al. 1997); terrestrial flightless invertebrates, especially those that are large, nocturnal and ground-dwelling; amphibians and reptiles that are nocturnal, ground-dwelling (Whitaker 1978), have low annual reproductive output (Towns 1994), and are oviparous, laying eggs in rookeries (Tyrrell et al. 2000); small terrestrial birds with weak flight and are surface or crevice nesters near ground level; small burrowing seabirds <250 g (Holdaway 1999) and surface-nesting seabirds such as tropic birds and terns.
2. *Vulnerable to Norway rats and ship rats in addition to the above*: small ground-nesting birds including well-flighted species; seabirds such as petrels and prions (Atkinson 1985); smaller ground-dwelling rodents.
3. *Vulnerable only to Norway rats in addition to the above*: seabirds 250–750 g (Holdaway 1999).
4. *Vulnerable only to ship rats in addition to 1 and 2 above*: diurnal ground-dwelling reptiles including some snakes (Daltry et al. 2001); small arboreal birds, especially hole nesting passerines and parakeets (Atkinson 1985); small marsupials and ground-dwelling or ground-foraging bats.

With well-conceived projects that include rigorous measurement of the responses to rat eradications, it may be possible to generate models of rat effects for a range of species and locations. Without such models, the motives and justification for rat eradications will continue to be questioned.

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