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To cite this article: D. R. Towns & Charles H. Daugherty (1994) Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation, New Zealand Journal of Zoology, 21:4, 325-339, DOI: [10.1080/03014223.1994.9518003](https://doi.org/10.1080/03014223.1994.9518003)

To link to this article: <http://dx.doi.org/10.1080/03014223.1994.9518003>



Published online: 30 Mar 2010.



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Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation

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Abstract Evidence from subfossils and from present distributions confirming range contractions and extinctions of New Zealand amphibians and reptiles is consistent with that from New Zealand landbirds, in which 40% of the fauna, including the largest species, has become extinct in the 1000 years since human arrival. The largest extant species of all higher taxa of herpetofauna—leiopelmatid frogs, tuatara, skinks, and geckos—are extinct on the mainland; 41% of the extant fauna (27 of 65 species) survive largely or entirely on rat-free offshore islands; and many species are now restricted to a few isolated locations, remnants of once wider distributions, a pattern called “secondary endemism”. Habitat alterations and occasional human predation may have contributed to range contractions, but the primary factor in extinctions is almost certainly introduced mammals, especially rats. At least three lines of evidence support this view: (1) species diversities and population densities are both far higher on rat-free islands than on mainland sites and rat-inhabited islands; (2) nocturnal species have suffered far more than diurnal ones—all populations of tuatara, two of four*

species of frogs, the largest *Cyclodina* skinks, and the largest species of *Hoplodactylus* geckos are now restricted to islands, most rat-free; (3) lizard populations on islands from which rats have been exterminated have shown rapid increases in range of habitats occupied, densities attained, and in reproductive success.

Keywords frogs; tuatara; geckos; skinks; *Leiopelma*; *Sphenodon*; *Hoplodactylus*; *Naultinus*; *Cyclodina*; *Leiopisma*; habitat destruction; introduced mammals; islands; predation; conservation; restoration

INTRODUCTION

Present concerns about catastrophic species declines—the “global biodiversity crisis”—are largely centred on continental areas, especially in the tropics. These declines appear particularly tragic because they are the direct effect of human activities that cause habitat loss, and which, with sufficient political will and foresight, could be stopped. However, they have been foreshadowed by similar biodiversity crises centred on island archipelagos, crises which in some areas began several thousand years ago and went unrecorded until they were revealed by recent archaeological or paleontological evidence.

Species declines on archipelagos can be attributed either to direct human effects, such as the destruction of forest habitats on Easter Island, and the over-exploitation that extinguished birds such as the great auk (*Alca impennis*) and dodo (*Raphus cucullatus*), or to indirect effects of human actions, such as the introduction of alien species that eliminate resident taxa. As we show in the following review, the

*Currently, three extant species of *Leiopelma* are recognised, but the Maud Island frog, regarded as *L. hamiltoni*, is likely to be described as a separate species, based on allozyme electrophoresis (B. D. Bell, C. H. Daugherty, J. M. Hay unpubl.) – Editor.

problem of indirect human effects has become the primary concern on many islands, especially in the New Zealand archipelago.

Several extinctions and many range contractions were recorded in the New Zealand avifauna during the first 200 years of European colonisation. These declines were well known amongst Victorian ornithologists, who regarded the New Zealand avifauna as "one of the most interesting and instructive in the world..." and whose "inevitable doom of surviving members" will be viewed with regret (Sibson in Hayman 1984). However, these declines were not unusual amongst the birds of island archipelagos. Over 90% of the birds that have become extinct since A.D. 1600 were island species (King 1984). This total includes 40% of the New Zealand terrestrial avifauna extinguished since the arrival of humans 1000 years ago (Atkinson & Millener 1991). Losses from New Zealand were exceeded in Hawaii, however, where at least 68% of the avifauna became extinct through the direct and indirect effects of prehistoric human cultures (Freed et al. 1987).

Unlike many other island archipelagos, New Zealand is distinctive because it is a continental fragment. Many vertebrate taxa were widely dispersed through the archipelago, so, unlike true oceanic islands, there is little site-specific island endemism, except among offshore island groups such as the Kermadec, Three Kings, Chatham, and subantarctic islands (Townes & Ballantine 1993). Also, unlike other temperate oceanic archipelagos, the amphibians and reptiles (especially lizards) have diversified into numerous species occupying a wide variety of habitats (Townes et al. 1985). As a result, New Zealand probably has the most diverse lizard fauna of any temperate archipelago on Earth (Daugherty et al. 1990a).

In this paper we review evidence for changes in the distribution of elements of the herpetofauna since the arrival of Polynesians and Europeans, describe known extinctions since human occupation, and examine the causes of both the extinctions and the population declines. We also compare range reductions and extinctions recorded in the herpetofauna with those in the avifauna.

NEW ZEALAND HERPETOFAUNA

Extinct fossil terrestrial groups and species

The first fossil remains of an ancient terrestrial New Zealand herpetofauna were unearthed in the early

1980s, with the discovery of a bone fragment of a theropod dinosaur. Subsequently, fossil bones of pterosaurs, allosaurs, ankylosaurs, and hypsilophodonts have been discovered by J. Wiffen (Cox 1991), all from the Late Cretaceous Haumurian Formation (66.5 m.y. B.P.) of the eastern North Island. The presence of these fragmentary dinosaur fossils provides further evidence of the Gondwanan links of the early New Zealand vertebrate fauna. However, although the extant sphenodontids seem universally regarded as an archaic Gondwanan element in the fauna (e.g., Bell et al. 1985; Stevens et al. 1988), early fossils of this group have yet to be found in New Zealand.

The known recent terrestrial herpetofauna of New Zealand comprises 71 species, six of which (three species each of frog and lizard) are presumed extinct (Table 1). However, of the lizards presumed extinct, only one, *Cyclodina northlandi*, is at present known in subfossil deposits (Worthy 1991). The skink *Leiopisma gracilicarpus* was described as a presumed juvenile attributed to the "kawekaweau", a large lizard reported by Maori and early European explorers (Hardy 1977). The single known specimen was subsequently found to be a sexually mature male (D. Townes pers. obs.) and could therefore be of an extant species. A New Zealand origin for the gecko *Hoplodactylus delcourti* was assumed by Bauer & Russell (1986) because of its morphological affinities with other members of the genus and its

Table 1 Species diversity estimates of the recent extant and extinct New Zealand terrestrial herpetofauna (includes species for which descriptions are still to be published). Data on species numbers are from Daugherty et al. (1994).

Taxon	Extant species	Extinct species	Percent extinct
Frogs: Leiopelmatidae			
<i>Leiopelma</i>	4	3	43
Tuatara: Sphenodontidae			
<i>Sphenodon</i>	2	–	–
Lizards: Gekkonidae			
<i>Hoplodactylus</i>	22	1*	4.5
<i>Nautinus</i>	7	–	–
Lizards: Scincidae			
<i>Cyclodina</i>	8	1	12.5
<i>Leiopisma</i>	22	1†	4.5
Total lizards	59	3	5.1
Total herpetofauna	65	6	9.2

*One species, *Hoplodactylus delcourti*, for which evidence of a New Zealand origin is still circumstantial.

†One species, *Leiopisma gracilicarpus*, whose taxonomic affinities remain unclear.

similarities with anecdotal reports of the kawekawea (Bauer & Russell 1988), but definitive evidence for this relationship has yet to be found in New Zealand. Subfossil remains (a jaw bone and a possible cloacal bone) described by Hutton (1899) from the South Island that might be attributable to *H. delcourti* (Bauer & Russell 1988) are apparently no longer in existence (the jaw bone), or cannot be used for species level identification (the cloacal bone) (A. H. Whitaker pers. comm.).

Extensive subfossil vertebrate deposits have been identified from caves and sand dunes around the North and South Islands of New Zealand. The oldest deposits that include the remains of frogs, tuatara, and lizards originated c. 14 000 yr B.P. (Worthy 1987b). There is, therefore, a gap in the fossil record from the Late Cretaceous to the late Pleistocene, the period in which all presently endemic elements in the herpetofauna must have arisen or arrived.

Prehuman distributions

Evidence of range contractions of many species can be obtained from analysis of the subfossil remains and those now identified from Maori midden sites, because they span the period before and during the arrival of humans in the New Zealand archipelago. However, if the effects of human occupation on the New Zealand herpetofauna are to be identified, it is necessary first to determine whether range contractions were either already underway or had begun

shortly before humans arrived. For example, there must have been substantial distribution changes for many species on the North and South Islands during the last glaciation, and some may have continued until flooding of Cook Strait was complete at c. 12 000 yr B.P.

No evidence of range reductions of reptiles before the arrival of humans in New Zealand has yet been found. However, natural range reductions due to climate change are conceivable for the frog *Leiopelma hochstetteri*, once distributed over the North Island and north-western South Island (Worthy 1987b), but now confined to the northern half of the North Island. Subfossil *L. hochstetteri* are present in old deposits (10 000–14 000 yr B.P.) in the South Island and are widespread in the central and northern North Island (Worthy 1987b). Now that extant populations of these frogs have been found in the western central North Island, the present North Island distribution of *L. hochstetteri* closely resembles that of subfossil deposits dated between $11\,050 \pm 50$ and 1680 ± 50 yr ago (Worthy 1987b). The arrival of the first humans and their commensal mammals 1000 yr B.P. appears to have affected both islands equally (see below), so should have affected *L. hochstetteri* on both islands in the same way. Since this is not the case, either *L. hochstetteri* disappeared from the South Island some time during the last 10 000 years (not necessarily due to human influences) or they are still present but have not been

Table 2 Current conservation status of the New Zealand herpetofauna based on the priority ranking system (Categories A–C) of Molloy & Davis (1992), with additional species (R/T)¹ based on Bell (1986).

Category: A	B	C	R/T
Frogs			
<i>L. hamiltoni</i> ²	<i>L. archeyi</i>		
<i>L. n.sp.</i> ²	<i>L. hochstetteri</i>		
Tuatara			
<i>S. guntheri</i> ²	<i>S. punctatus</i> ²		
Lizards			
<i>C. n. sp. 1.</i> ²	<i>C. macgregori</i> ²	<i>C. alani</i> ²	<i>H. duvaucelii</i> ²
<i>H. kahutarae</i>	<i>C. whitakeri</i>	<i>C. n. sp. 2.</i> ²	<i>N. rudis</i>
<i>L. grande</i>	<i>H. chrysosireticus</i>	<i>L. n. nigriplantare</i> ³	<i>N. tuberculatus</i>
<i>L. otagense</i> "otagense"	<i>H. rakiurae</i> ³	<i>L. notosaurus</i> ³	<i>C. oliveri</i> ²
<i>L. homalonotum</i> ²	<i>H. stephensi</i> ²	<i>L. stenotis</i> ³	<i>L. fallai</i> ³
	<i>L. n. sp.</i>		
	<i>L. microlepis</i>		
	<i>L. otagense</i> "waimatense"		
	<i>L. striatum</i>		

¹The categories "rare" and "regionally threatened" of Bell (1986).

²Island pseudoendemics.

³Island endemics (including species of the Stewart Island region).

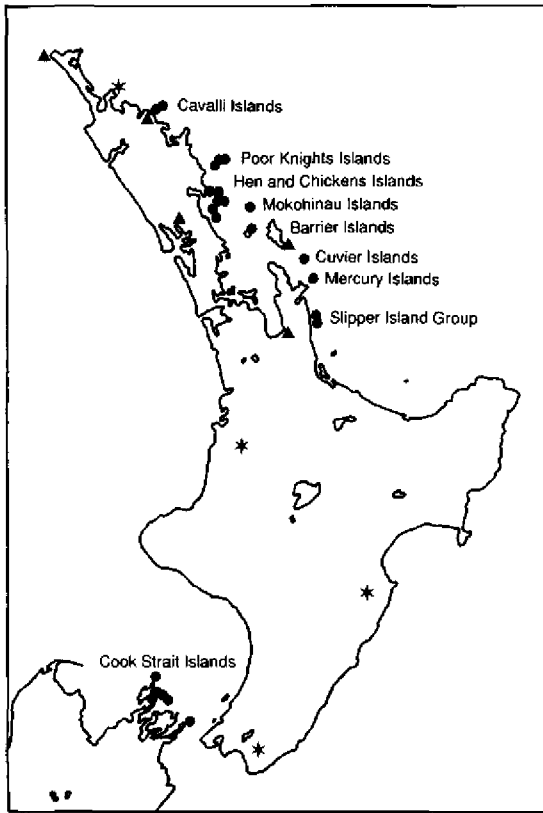


Fig. 1 Distribution of extant and extinct populations of Duvaucel's gecko (*Hoplodactylus duvaucelii*) with data from Pickard & Towns (1988) and Worthy (1987c); extant populations (dots), historic records presumed extinct (triangles), and subfossil records (star).

located. The latter is a possibility, since substantial populations of *L. hochstetteri* sympatric with a frog similar to *L. archeyi* were discovered in the western North Island only in 1991 (Thurley & Bell 1994).

Present status of herpetofauna

Almost half (47%) of the New Zealand herpetofauna is listed as endangered, rare, or threatened, as assessed either from IUCN categories (Bell 1986) or by extrapolating from a priority ranking system (Molloy & Davis 1992). This total comprises all frogs and tuatara and 40% of the lizards (Table 2). The proportion of lizards listed is likely to increase as new taxonomic studies reveal previously unknown species with restricted distributions.

Three lines of evidence indicate that most species now regarded as threatened have become so because of past catastrophes on the mainland.

1. Much of the fauna (36%) is now largely or totally confined to offshore islands. The threatened species confined to islands comprise half of the frog species, both tuatara species, and 13 of the 24 (54%) lizard species (Table 2). However, comparison of present distributions with subfossil Holocene deposits in caves, dunes, and middens, indicates that of the species now on islands—both frogs, the tuatara, and six lizards (25% of the threatened species)—are secondary endemics or pseudoendemics (Daugherty et al. 1990a), species that were once present, some of them widely, on the mainland. Most island species therefore represent relictual distributions. The few primary (true) endemics are on the Three Kings Islands (*Leiolopisma fallai*), Poor Knights Islands (an undescribed species of *Cyclodina*), Stewart Island (*Hoplodactylus rakiurae* and at least two species of *Leiolopisma*), and the Chathams Islands (*Leiolopisma n. nigriplantare*).

2. Unlike narrow distributions of primary endemics, the pseudoendemics have a wide and often erratic distribution, sometimes with isolated populations separated by several hundred kilometres. Considerable range contractions can be inferred when the present distribution of these isolated populations is compared with widespread subfossil material for species such as tuatara (*Sphenodon* spp.), Duvaucel's gecko (*Hoplodactylus duvaucelii*), robust skink (*Cyclodina alani*), and Whitaker's skink (*C. whitakeri*).

Tuatara remains have been recorded over much of the North and South Island of New Zealand, and small populations of living tuatara were reported on the mainland North Island until late in the nineteenth century (Cree & Butler 1993). The genus is now confined to 29 islands scattered between Cook Strait and north-eastern New Zealand (Cree & Butler 1993, fig. 1, 2). Remains of Duvaucel's gecko, robust skink, and Whitaker's skinks have been found in caves and dune deposits at many sites on the North Island. Associated fauna include lizards and land snails that inhabit damp, broadleaf forest (Worthy 1991), a habitat that would once have covered extensive areas of the North Island. Duvaucel's gecko is now known from 36 islands from Cook Strait to Northland (Towns 1991) (Fig. 1); robust skinks are now confined to six small islands with a total area of about 33 ha (Fig. 2); and natural populations of Whitaker's skinks are confined to two islands and a small mainland site with a combined area of <20 ha (Towns 1992).

3. Unlike the high levels of divergence shown

between primary endemics of different islands, island populations of pseudoendemics often show very little divergence over considerable distances. For example, the primary island endemic *Leiopisma fallai* has a high level of genetic differentiation from all other species (Nei's $D > 0.2$). By comparison, three populations of *C. whitakeri* show no differentiation at all between two island populations off the Coromandel Peninsula and a third on the Wellington coast 500 km further south ($D = 0$), and the maximum level of differentiation is barely measurable for other skinks and tuatara (e.g., *L. moco*, six populations, $D < 0.02$; *Sphenodon punctatus*, 19 northern populations, $D < 0.03$) (Daugherty et al. 1990b; C. H. Daugherty pers. obs.). This low divergence over wide geographic distances is consistent with the hypothesis that these scattered populations are small remnants of a formerly much larger gene pool, such as those formed when sea levels rose at the end of the last glaciation and isolated fragments of mainland communities on the remaining high ground. These remaining isolates, combined with subfossils on the mainland and some larger islands, provide a means of defining the extent of the community depletion on the mainland over the past 1000 years. The islands have also provided a means of testing some of the likely causes of the declines.

Assemblages past and present

Apart from its unusual archaic elements, the New Zealand herpetofauna is unique in two respects: sympatric species diversity is unusually high for a temperate area, and local assemblages comprise an unusually large number of congeneric species.

The best examples of this diversity on the main islands are now found at middle altitudes (600–1000 m a.s.l.) in native tussocklands of the south-eastern South Island (Table 3), where up to six species of *Leiopisma* skinks and a species of *Hoplodactylus* gecko co-exist in rocky outcrops and vegetation (Towns et al. 1985; Patterson & Daugherty 1990; Patterson 1992; R. Hitchmough pers. comm.).

Even higher diversities have been recorded on some of the north-eastern offshore islands. For example, 13 species of lizards and one species of native frog were found on 27 761 ha Great Barrier Island (Newman & Towns 1985). However, no small island in the New Zealand area exceeds the combined density and diversity of lizards found on Middle Island (Mercury Islands), with 10 species of lizards and tuatara on an island of 13 ha. This

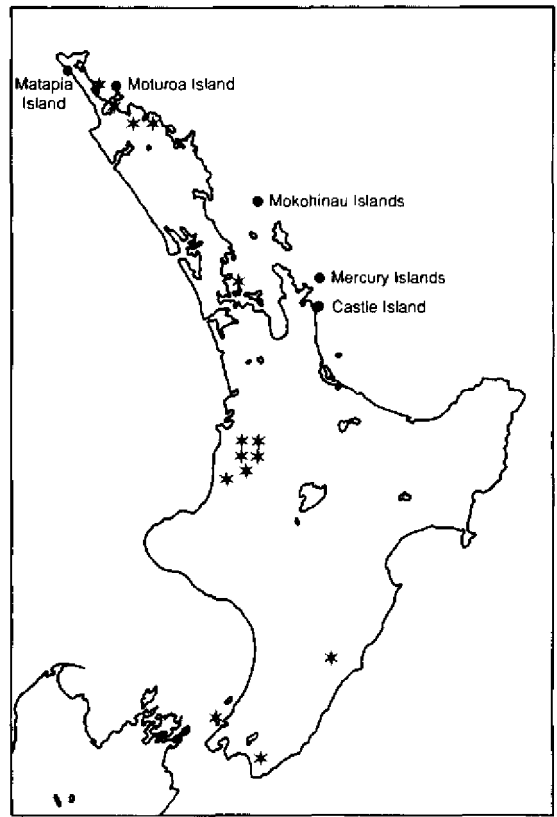


Fig. 2 Distribution of extant and extinct populations of robust skink (*Cyclodina alani*) after Towns (1992) and with additional data from I. McFadden (pers. comm.). Conventions as in Fig. 1.

fauna includes three species each in *Hoplodactylus* and *Leiopisma* and four species in *Cyclodina* (Towns 1991).

The diverse extant island assemblages are overshadowed by the extraordinary herpetofauna once present in the northern North Island (Table 4), which originally had 22 sympatric species including four species of *Leiopelma* frogs and at least six (possibly seven) species of *Cyclodina* skinks. Over 60% of these species have since disappeared from the area. Most of the eight species that remain persist only in low numbers and in scattered localities.

CAUSES OF RECENT RANGE REDUCTIONS

Three (possibly four) species of frogs and tuatara (but no lizards) are known to have disappeared from

the South Island since the arrival of humans, compared with two species of frogs, tuatara, two species of geckos, and five species of skinks from the North Island. Differences in extinction rates of the northern and southern faunas appear to reflect differences in habits and size of the animals. A far higher proportion of the lizard fauna in the north was nocturnal or crepuscular (77%) than in the south (36%). This was especially apparent in the skinks, where only 34% of the northern fauna was diurnal compared with 100% of the fauna in the south (Tables 3, 4). In addition, some of the northern forms were very large, including possibly the world's largest gecko (although the cloacal bone identified by Bauer & Russell (1988) could indicate the former presence of a giant gecko in the South Island), and some very large skinks. Almost all of the largest forms have since disappeared from Northland (including some diurnal species that have survived elsewhere). However, on northern offshore islands (such as Middle Island) that have little evidence of human modification, 82% of the terrestrial reptile species (tuatara and lizards) are nocturnal or crepuscular, including some of the large lizards that are now known to have disappeared from Northland (Towns et al. 1985).

The comparisons therefore indicate that the historic extinctions have been somewhat localised, and that the most vulnerable species were those that are nocturnal or crepuscular and of large body size (Whitaker 1978).

Direct human effects

Sudden declines in diversity of the New Zealand

terrestrial vertebrate fauna coinciding with the arrival of humans have been noted for many years (e.g., Fleming 1962; Whitaker 1978; Worthy 1987b; Atkinson & Millener 1991). However, the extent of the decline in herpetofauna has only recently become apparent. For example, Whitaker (1978) predicted that about 18 lizard species once inhabited the North Island, whereas recent taxonomy and subfossil discoveries have increased this to 30 species, 30% of which have either disappeared from the mainland or are reduced to a few scattered populations.

There is no evidence that predation by humans was the direct cause of the disappearance of any of these species. Tuatara and several lizard species appear in Maori middens (e.g., Nichol 1988) but, with the exception of tuatara (which may occasionally have been eaten), lizards were more likely to have been attracted to middens by decaying meat (especially shellfish) and become trapped there.

There was intensive harvesting of tuatara to provide specimens for museums during the late nineteenth century until the practice was stopped by legislation protecting the species in 1895 (Newman 1987). Only one population of tuatara (East Island) may have been lost as a result of this trade (Cree & Butler 1993).

Indirect human effects

Habitat destruction

Historic and prehistoric declines of much of the New Zealand vertebrate fauna were regarded as difficult to interpret as recently as the 1970s, with habitat loss, climate change, and disease introduced with European birds being invoked as the most likely

Table 3 Extant lizards of tussock grasslands in Central Otago, south-eastern South Island, with data on size (maximum snout-vent length (mm); SVL) from Hardy (1977), Towns (1985), Patterson & Daugherty (1990), Duggan (1991), and Hitchmough (pers. comm.) and habits defined as diurnal (D), and nocturnal (N).

Species	SVL	Habit	Habitat
<i>Hoplodactylus</i> spp.*	59-80	N	Rock outcrops, boulder piles
<i>Nautinus gemmeus</i>	71.7	D	Shrubs
<i>Leiopisma chloronoton</i>	108	D	Damp valleys
<i>L. grande</i>	108	D	Rock outcrops
<i>L. inconspicuum</i>	70	D	Herb and shrub cover
<i>L. maccanni</i>	72.5	D	Rocky areas
<i>L. nigriplantare polychroma</i>	77	D	Tussock cover
<i>L. otagense</i>	135	D	Rocky outcrops and stream canyons

*Complex of at least four species under review by R. Hitchmough.

causes (e.g., Williams 1973). However, although avian diseases might be implicated for birds, the declines also affected reptiles and even large insects.

Table 4 Herpetofauna of coastal broadleaf forest and associated shorelines in Northland (near Cavalli Islands) 1000 yr B.P., based on data from local extant species and subfossil deposits in dunes and caves. Data from Whitaker (1973), Hardy (1977), Robb & Rowlands (1977), Hitchmough (1982; pers. comm.), Barnett (1985), Bauer & Russell (1986, 1988), Castanet et al. (1988), Pickard & Towns (1988), and Worthy (1987a, c; 1991). Size is given as maximum snout-vent length (mm) (SVL); habits are defined as diurnal (D), crepuscular (C), and nocturnal (N); and status as still present (+), locally extinct (LEx), or extinct (Ex).

Species	SVL	Habit	Present status
Frogs			
<i>Leiopelma markhami</i>	60	N	Ex
<i>L. waitomoensis</i>	100	N	Ex
<i>L. archevi</i>	41	N	LEx
<i>L. hochstetteri</i>	45	N	LEx
Tuatara			
<i>Sphenodon punctatus</i>	180	N	LEx
Lizards			
<i>Hoplodactylus delcourti?</i>	370	N	Ex
<i>H. duvaucelii</i>	160	N	LEx
<i>H. granulatus</i>	93	D-N	+
<i>H. maculatus</i>	65*	N	+
<i>H. pacificus</i>	73*	N	+
<i>Naultinus grayi</i>	95	D	+
<i>Cyclodina aenea</i>	62	D-C	+
<i>C. alani</i>	115–125	N	LEx
<i>C. macgregori</i>	112	N	LEx
<i>C. northlandi</i>	160–170	N	Ex
<i>C. oliveri</i>	108	C-N	LEx
<i>C. ornata</i>	80	C	+
<i>Leiopelma homalonotum</i> †	131	D	LEx
<i>L. infrapunctatum</i> ‡	75	D	LEx
<i>L. moco</i>	72	D	LEx
<i>L. smithi</i>	77	D	+
<i>L. suteri</i>	108	N	+
Total recorded	22	Total	8 remaining

*Mean measurements only available.

†*Leiopelma homalonotum* was identified as possibly present in deposits by Worthy (1991) and survives on Hauraki Gulf islands in forests similar to those found in Northland.

‡Worthy (1991) identified *Leiopelma infrapunctatum* (now known from the central and southern North Island and South Island) from caves in Northland. However, another forest-inhabiting species of similar size, *L. striatum*, recorded from Northland (Pickard & Towns 1988), was not identified by Worthy from subfossil deposits.

Many extinctions were too recent to be attributable to climate change, and forest species (such as tuatara and large *Cyclodina* skinks) disappeared where extensive tracts of forest remained.

Habitat loss, such as removal of forest, by itself probably caused few (if any) extinctions in the herpetofauna. In fact, some forest species such as tuatara apparently reach artificially high densities when areas of forest are converted to pasture (Cree & Butler 1993). On the other hand, habitat modification has resulted in several documented range contractions. For example, the two remaining native frog species on the North Island (*Leiopelma archevi* and *L. hochstetteri*) both require forest or shrub cover to retain moist substrata (*L. archevi*) and minimise siltation of streams (*L. hochstetteri*). Degradation of streams following removal of forest cover was identified as a particular problem faced by *L. hochstetteri* (Bell 1985), and is possible even under forest cover if introduced browsers (such as pigs and goats) are abundant (Newman & Towns 1985). Nonetheless, these frogs have shown considerable resilience, and they have survived (or recolonised) streams in the Coromandel Peninsula that have been damaged by gold mining (siltation from sluicing) and kauri milling (damming, flooding, and scouring).

Recent habitat destruction may have affected the skink *Leiopelma striatum* that apparently lives mainly in forests. When forests on the western central North Island were cleared for grazing, the skinks managed to survive amongst tree stumps in rough pasture. In some areas, stumps and logs were among the few strongholds of the species, until the past decade when the logs rotted away or were removed for pasture improvement (Robb 1980; Whitaker 1993). The present distributional range of the species is unclear, and it is now seldom seen (Whitaker 1993).

The most carefully documented range declines have been of the South Island "giant" skinks, *Leiopelma grande* and *L. otagense*. Intensive surveys for these saxicolous (rock-dwelling) species over 1.46 million ha of potential habitat in outcropping fractured schist (including known historic strongholds) between 1984 and 1989 revealed giant skink populations in only 140 000 ha (8% of the area). Some previously known populations had disappeared within the last few decades (Whitaker & Loh 1990). Both historic and present declines were attributed to habitat modification through farming practices that changed from extensive pastoralism of native grasslands to oversowing with exotic grasses and intensive grazing. This change

appears to have unleashed a complex series of effects including removal of shrub cover around outcrops (a source of berries for lizards), alteration of invertebrate faunas, reduction of cover and hence loss of refuges against predators (especially feral cats), disturbance and fouling of habitats by stock, and denudation of vegetation by rabbits (Whitaker & Loh 1990).

Predation

Suggestions that predation by introduced rodents (especially the Pacific rat, *Rattus exulans*) might have played a major role in declines of mainland birds were initially either greeted with scepticism (e.g., Williams 1973) or looked at as an interesting proposition (Gibb & Flux 1973); data implicating Pacific rats in the local extinction of lizards and recruitment failure of tuatara were still regarded recently as equivocal by some (e.g., Craig 1986).

The appearance of Pacific rats in New Zealand accompanying the arrival of Maori 1000 years ago only foreshadowed what was to come. Between 1790 and 1885, an array of mammalian predators was introduced into a herpetofauna previously exposed to predation largely by birds and reptiles (Table 5). Local and temporal variation in the consequences has resulted in an extremely complex situation on the mainland, where the effects of different kinds of introduced predators are difficult to disentangle. However, many of the offshore islands have fewer introduced potential predators than the mainland (often just one), and these situations allow assessment of the effects of individual species.

Table 5 Sequence of introductions of known mammalian predators of New Zealand amphibians and reptiles with data from Atkinson (1973) and King (1990). Reported introduction dates may vary between the North and South Islands.

Species		Date of introduction (A.D.)
Pacific rat	<i>Rattus exulans</i>	c. 1000
Dog	<i>Canis familiaris</i>	c. 1000
Pig	<i>Sus scrofa</i>	1790–1840
Norway rat	<i>Rattus norvegicus</i>	1790–1850
Mouse	<i>Mus musculus</i>	1830–1850
Cat	<i>Felis catus</i>	1830–1850
Ship rat	<i>Rattus rattus</i>	1860–1890
Ferret	<i>Mustela furo</i>	1879–1890
Weasel	<i>Mustela nivalis vulgaris</i>	1885–1886
Stoat	<i>Mustela erminea</i>	1885–1886

Pacific rats (kiore): Despite (or perhaps because of) initial scepticism, Pacific rats have been implicated in the demise of many species of vertebrates and invertebrates on the mainland (Atkinson & Moller 1990). However, a relatively small number of mainland extinctions of herpetofauna can be attributed to Pacific rats alone.

Of three species of extinct native frogs, one, *Leiopelma markhami*, appears in cave deposits over both the North and South Islands, and the second, *L. waitomoensis*, was widespread through the North Island. Two extant species, *L. hamiltoni* and an undescribed near relative, are confined to single rodent-free islands, although *L. hamiltoni* (or its near relatives) was once widespread in the North Island and South Island. These species appear to have disappeared from the main islands in the last 1000 years; the most recent remains of *L. markhami* were dated at 300 yr B.P. (Worthy 1987b). The ages of known deposits suggest that Pacific rats are the most likely cause of these species' declines and extinctions (Worthy 1987b).

Similarly, two lizard species (*Cyclodina alani* and *C. macgregori*), once widespread on the mainland, now exist only on islands free of all rodents (other than mice), and were therefore probably lost from the mainland soon after Pacific rats arrived. These two skinks and the three frogs probably represented the first wave of losses (either from the mainland only or as full extinctions).

For other species the relationship appears less consistent. For example, two species (*Cyclodina whitakeri* and *C. oliveri*) mostly survive on islands without rodents, but co-exist with rodents (and other introduced predators) in a few sites where the lizards inhabit deep boulder banks.

The disappearance of tuatara from the mainland has also been attributed to the affects of Pacific rats (e.g., Whitaker 1978). Whether (and for how long) the two can co-exist probably depends on many factors, one of which is the size of island, and therefore the availability of refuges for tuatara and their nests (Towns 1991). For example, no tuatara populations co-exist with Pacific rats on islands of <70 ha (Coppermine Island), yet there are several thriving populations of tuatara on rat-free islands of <10 ha. On the other hand, impaired or consistently failed recruitment of tuatara has been recorded on all islands (including Coppermine) with Pacific rats (Crook 1973; Cree et al. in press).

On the mainland, Pacific rats probably reduced juvenile recruitment into tuatara populations, but did not necessarily cause their extinction. However,

tuatara and a number of lizard species were almost certainly greatly reduced in abundance because of the presence of Pacific rats: experimental evidence for this is provided below.

Some of the effects of Pacific rats could be assessed from the response of resident lizards once the rats were removed, using rodenticide, from 18 ha Korapuki Island (Mercury Islands) in late 1986 (McFadden & Towns 1991). A small population of introduced rabbits was also removed by shooting in 1987. Soils, vegetation, invertebrates, lizards, and birds were surveyed in 1974 (Hicks et al. 1975), lizard surveys were repeated in 1985, and lizards and invertebrate diversity and abundance have been documented at least annually (for lizards, biennially) since 1986, with comparative data obtained from nearby islands naturally free of rodents (Towns 1991, 1994).

Before the Pacific rats were removed, lizard species diversity on Korapuki was half (five species) that recorded on a smaller neighbouring island (13 ha Middle Island) free of rats, and a far lower proportion of the lizards caught were nocturnal on Korapuki Island (2%) than on Middle Island (65%) (Towns 1991). Lizard relative abundance measured at equivalent coastal sites was significantly higher on Middle Island than on Korapuki Island while rats were present, but on Korapuki it increased up to 30-fold at some sites once rats were removed (Towns 1991, 1994). Significantly, the most rapid response on Korapuki Island was by diurnal shore skinks (*Leiopisma smithi*), previously thought to be less vulnerable to the effects of rats than nocturnal species (e.g., Towns et al. 1985). Similar responses by diurnal lizard species following removal of Pacific rats have now been recorded on Motuopao Island (Parrish & Pierce 1993) and in the Mokohinau Islands (I. McFadden pers. comm.).

A less rapid response was found in forested areas on Korapuki Island, but in these sites the previously rare crepuscular copper skink (*Cyclodina aenea*) is now up to 10 times more abundant than it was before removal of Pacific rats (Towns 1994).

A second test of the effects of Pacific rats was, following their removal, to reintroduce nocturnal and crepuscular lizard species judged to be vulnerable to predation. Four species of lizards in this category were almost certainly present previously on Korapuki Island, a reasonable assumption based on proximity and recent land connections of Korapuki Island to its neighbours (Middle and Green Islands) (Towns 1994). If these lizards were absent from

Korapuki because of habitat deficiencies rather than the effects of rats, the releases should fail.

Reintroductions of these four species to Korapuki Island from Middle and Green Islands are under way. The first of these, Whitaker's skink (*Cyclodina whitakeri*), has been followed for 5 years since release (Towns 1994). The released population has high adult survival, significantly higher body weight compared with length than other populations, and has successfully produced offspring for several years, resulting in a steady increase in estimated population size (Towns 1994). This is despite habitat degradation (reduced vegetation cover) as a result of the previous presence of rabbits. Unless there have been other unknown factors operating in the past, the presence of Pacific rats, rather than lack of suitable habitats, explains the reduced diversity, and reduced densities of lizards (especially of nocturnal species) previously recorded on Korapuki Island (Hicks et al. 1975; Towns 1991).

Dogs (kuri): Along with Pacific rats, Maori also introduced domestic dogs (*Canis familiaris*) to the New Zealand environment. Some are likely to have become feral and could have had a significant impact on ground birds, frogs, and reptiles (Anderson 1990). In the Galapagos Islands, feral dogs (descendants of European breeds) extirpated populations of the diurnal land iguanas (*Conolophus suberistatus*) on the island of Santa Cruz (H. Snell pers. comm. 1988). Whether dogs might have had similarly devastating effects on nocturnal burrow-inhabiting species such as tuatara (or on their nesting rookeries) remains unclear, although there is evidence that feral hybrids of Maori-European dogs fed on ground-dwelling birds during the nineteenth century (King 1984).

Pigs and Norway rats: The first mammals introduced to New Zealand by Europeans were pigs and Norway rats, in c. 1790 (Table 5). Wild pigs feed on lizards and tuatara (Towns & McFadden 1993), but where they have been introduced to offshore islands, their effects on reptiles appear to be transitory. For example, pigs were free ranging on Aorangi Island (Poor Knights Islands) from c. 1820 until their eradication in 1936 (Veitch & Bell 1990). However, tuatara and eight species of lizards survived on Aorangi. No significant differences between the diversity or densities of lizards or tuatara on Aorangi and neighbouring Tawhiti Rahi were recorded by Whitaker (1973, 1978), except that the island previously with pigs had one more species of skink than the one without.

Pigs are likely to have local effects on species that inhabit damp areas along streams (such as native frogs) and accumulations of litter (such as some skinks), but they may not be solely responsible for identifiable range contractions or extinctions of New Zealand amphibians or reptiles.

The Norway rat (*Rattus norvegicus*), the largest of the rat species in New Zealand, was the second to arrive (Atkinson 1973) and co-existed with Pacific rats on the mainland for at least 100 years. Norway rats are a ground-feeding species that will attack larger prey than Pacific rats, and they have an affinity for both fresh and salt water, in which they can swim up to 1.4 km (Atkinson & Moller 1990). They can have a devastating effect on the herpetofauna.

Whereas tuatara and Pacific rats may co-exist for considerable periods, tuatara are rapidly eliminated by Norway rats. For example, a dense population of tuatara which co-existed with mice on Whenuakura Island, disappeared within 2 years of the arrival of Norway rats (Newman 1986). Many lizards appear to be similarly affected; no lizards at all could be found on Motuhoropapa Island (Noises Islands) after the island was invaded by Norway rats in the late 1950s (D. Towns pers. obs.). Similarly, the Fiordland skink (*Leiopisma acrinusum*) is absent from small islands inhabited by Norway rats, but rapidly reinvaded Breaksea Island from a neighbouring rock stack once Norway rats were removed (Taylor & Thomas 1993).

Mice, cats, ship rats, and mustelids: The combined effects of Pacific rats and Norway rats are likely to have precipitated a second wave of extinctions (cf. Williams 1973), possibly including species such as tuatara and the large Duvaucel's gecko. However, the picture is complicated by the third wave of mammalian predators that arrived in New Zealand over the 50 years between 1830 and 1880. All of the species listed in Table 5 (including mice) are now known to prey on lizards (Newman 1988; King 1990; Daugherty & Towns 1991). Losses to mice, cats, ship rats, and mustelids must have represented an intolerable burden on populations of reptiles already depleted by Pacific and Norway rats (and possibly dogs). However, whereas arboreal species had been relatively safe from predation by the predominantly ground-feeding Norway rats and cats, they had no refuge from the arboreal ship rats and mustelids that were introduced in mid to late nineteenth century, and which could reach both terrestrial and non-terrestrial species.

The combined effects of habitat destruction and the waves of introductions of predators (possibly

including some introduced birds) would have completed the demise of any vulnerable species still retaining a tenuous existence on the mainland, and were doubtless responsible for the fragmentary distributions now shown for many of those that survive.

DISCUSSION

Comparison with birds

The decline of birds on mainland New Zealand concurrent with the arrival of humans is less difficult to chart than that of amphibians and reptiles; the birds were conspicuous and their habits and fate since European colonisation were followed by early naturalists. In contrast, when Europeans arrived, the herpetofauna had already become so inconspicuous that only 29 (41%) of the currently known 71 extinct or extant species were described before 1970. Some of the largest species in the fauna were discovered in the last 25 years (e.g., *Cyclodina alani*, *C. macgregori*), but were previously unknown because of their fragmented distribution restricted to small islands.

In the period A.D. 1000–1769 (before Europeans and their commensal pests had arrived), the mainland New Zealand avifauna had already lost all 11 species of moa, seven species of large waterfowl, five species of rails, three species of raptors, a pelican, a coot, a crow, an owlet-nightjar, a merganser, a snipe, and (probably) four wrens (King 1990; Atkinson & Millener 1991). The larger species (such as moa and some of the flightless waterfowl) may have been hunted to extinction, but the smaller species were most likely extirpated by rats. Some of these species (including a wren) were flightless or almost so (Atkinson & Millener 1991).

The herpetofauna suffered losses like those recorded for birds, with the total extinction or loss from the mainland of five species of frogs and at least two species of lizards. The time of disappearance of the large skink *Cyclodina northlandi* is unknown (Worthy 1991). The most vulnerable section of the herpetofauna was the frogs, which between A.D. 1000 and 1769 apparently lost 43% of their species (a larger proportion than that of birds), probably because of the frogs' large size and nocturnal habits (Worthy 1987b). Unlike birds, a large number of reptile and frog species (17) survived on islands (Daugherty et al. 1994). Without these island survivors, New Zealand would have lost

32% of its herpetofauna—little less than the 40% extinction documented for birds.

Studies of the island populations of reptiles have revealed several additional biological characteristics that increase their vulnerability to predation. These include slow growth rates (especially in large geckos and tuatara) and low annual reproductive output, which result in low intrinsic rates of increase (Towns 1994; Cree 1994); and in some species of *Cyclodina* and tuatara, high cutaneous water loss that ties them to damp environments (Cree & Daugherty 1991). Birds may have had fewer physiological impediments than reptiles, but the flightless species would have shared the high-risk ground-nesting habits shown by tuatara.

Simple versus complex causes of decline

The current sudden declines of global herpetofauna, especially frogs, have evoked many attempts to define a cause. The declines on archipelagos often predate by many centuries those of continental amphibians and may provide lessons that can be applied elsewhere. Archipelagos provide relatively simple systems that have undergone waves of extinctions, often as a result of similar combinations of factors at widely separated locations. Analyses of the extinctions and range reductions in New Zealand show that many factors may be involved, influencing different species in different ways.

The effects of habitat loss have been a relatively recent problem for the New Zealand herpetofauna (but not necessarily for the avifauna) and, given the right kind of effort, could be reversed. However, the subtle effects of predation are widely experienced in archipelagos. These are difficult to ameliorate and may even be difficult to interpret. For example, mustelids are rightly regarded as extremely voracious and efficient predators (King 1990). However, their release on the North and South Islands of New Zealand probably postdated the major devastation of the herpetofauna caused by three species of rats, mice, and cats (King 1984). Similarly, declines of ground lizards, racer snakes, and skinks in the Windward Islands (West Indies), although frequently attributed to mongoose (*Herpestes auro-punctatus*), may in fact have been caused by ship rats, which arrived in the islands before the mongooses were liberated (Corke 1992).

The rising lid: initiatives on islands

Many members of the New Zealand herpetofauna that have survived the crises of the last 1000 years now have improved prospects for the future resulting

from legislative changes, recent research, and new conservation initiatives. For example, legislation passed in 1987 that protects almost all remaining native forests under Government control has resolved a continuing threat for native frogs: degradation of stream catchments due to deforestation (Bell 1985). There have been surprise discoveries of native frogs inhabiting high altitude native ferns and grasses (Thurley & Bell 1994). One species, *L. hochstetteri*, presents some conservation challenges with the discovery that different populations may have been separated for considerable periods and now have different complements of unique supernumerary chromosomes (Green 1994); conservation efforts may therefore need to be based on individual populations or identified metapopulations rather than on the species.

New initiatives on islands, including eradication of introduced mammals and restoration of depleted communities, could improve the conservation status of >70% of the presently listed threatened species of amphibians and reptiles.

By the end of 1994, at least 20 predator eradication campaigns on islands will have been completed that benefit New Zealand reptiles, producing a total of 2400 ha of habitat free of predatory mammals. Many resident species of reptiles that have been reduced to low densities by predators are now increasing in abundance on islands in response to the removal of predators (mainly rats). Some of these, including *Leiopisma suteri*, *L. moco*, *L. acrinasum*, and *Hoplodactylus duvaucelii*, are now rare or extinct on the mainland. Populations of some species had been reduced to critically low numbers before the campaigns against predators were instigated. Direct benefits from these campaigns should soon be visible for *Cyclodina macgregori*, severely affected by mice on Mana Island (Newman 1994), and *Sphenodon punctatus*, affected by recruitment failure in the Chickens Islands (Cree et al. in press) and reduced to tiny relict populations (20 individuals or less) by Pacific rats on Cuvier Island and in the Mercury Islands (Towns et al. 1993, 1994). Further, the campaigns against predators have restored damaged island habitats that are now suitable places to which rare species can be reintroduced. These restoration projects began in 1988 with reintroduction of *Cyclodina whitakeri* to Korapuki Island (Mercury Islands), and were extended in 1992 to include *C. alani*. By 1996, *Sphenodon guntheri* should have been reintroduced to one (possibly two) islands in the Cook Strait region. Most importantly, these campaigns against

exotic predators, followed by reintroduction of reptiles, aim to restore the unique interactions in unusual plant-invertebrate-reptile-seabird systems (Daugherty et al. 1990a; Towns et al. 1990). These gains, and others still planned, will not only improve the status of species on islands, but will also improve the security of species vulnerable to rodents (such as the endemic *Leiopisma fallai* of the Three Kings islands) through the development of techniques that prevent rodent invasions.

However, while many species will benefit, the initiatives on islands need to be placed in perspective: successes on islands will still at best only restore most species to a fraction of their previous range. For the foreseeable future, the remaining 90% of the range of species now confined to islands—the mainland—will be inaccessible because introduced predators can only be controlled locally, at considerable cost, and for short periods. Similar problems bedevil the larger islands in archipelagos throughout the world (Atkinson 1989). On the other hand, unlike the insoluble problems caused by the indirect effects of humans on some archipelagos, much habitat modification and destruction on continents can be reversed (such as in restoration of dry tropical forest in Costa Rica) (Janzen 1986), despite the vast scale of habitat destruction in many areas (Janzen 1988).

ACKNOWLEDGMENTS

We are grateful to the Department of Conservation and to Victoria University of Wellington for their respective support to attend the Second World Congress of Herpetology (Adelaide, South Australia) where a draft of this paper was presented. Our thanks also to James Vial for the invitation to present the paper at the symposium on "Contractions of ranges, disappearance and extinction", and to Ian Atkinson, Rod Hitchmough, Tony Whitaker, and Kim King for comments on the draft manuscript.

REFERENCES

- Anderson, A. J. 1990: Kuri. *In: King, C. ed. The handbook of New Zealand mammals.* Auckland, Oxford University Press. Pp. 281–287.
- Atkinson, I. A. E. 1973: Spread of the ship rat (*Rattus r. rattus*) in New Zealand. *Journal of the Royal Society of New Zealand* 3: 457–472.
- Atkinson, I. A. E. 1989: Introduced animals and extinctions. *In: Western, D.; Pearl, M. C. ed. Conservation for the twenty-first century.* New York, Oxford University Press. Pp. 54–79.
- Atkinson, I. A. E.; Millener, P. R. 1991: An ornithological glimpse into New Zealand's pre-human past. *Acta XX Congressus internationalis ornithologici* vol. 1. Pp. 127–192.
- Atkinson, I. A. E.; Moller, H. 1990: Kiore. *In: King, C. ed. The handbook of New Zealand mammals.* Auckland, Oxford University Press. Pp. 175–192.
- Barnett, S. 1985: *New Zealand in the wild.* Auckland, Collins. 128 p.
- Bauer, A. M.; Russell, A. P. 1986: *Hoplodactylus delcourti* n. sp. (Reptilia: Gekkonidae), the largest known gecko. *New Zealand journal of zoology* 13: 141–148.
- Bauer, A. M.; Russell, A. P. 1988: Osteological evidence for the prior occurrence of a giant gecko in Otago, New Zealand. *Cryptozoology* 7: 22–37.
- Bell, Ben D. 1985: Conservation status of the endemic New Zealand frogs. *In: Grigg, G.; Shine, R.; Ehmann, H. ed. The biology of Australasian frogs and reptiles.* Royal Zoological Society of New South Wales. Pp. 449–458.
- Bell, B. D.; Newman, D. G.; Daugherty, C. H. 1985: The ecological biogeography of the archaic New Zealand herpetofauna (Leiopelmatidae, Sphenodontidae). *In: Grigg, G.; Shine, R.; Ehmann, H. ed. The biology of Australasian frogs and reptiles.* Royal Zoological Society of New South Wales. Pp. 99–106.
- Bell, Brian D. 1986: The conservation status of New Zealand wildlife. *New Zealand Wildlife Service occasional publication* 12.
- Castanet, J.; Newman, D. G.; Saint Girons, H. 1988: Skeletochronological data on the growth, age, and population structure of the tuatara, *Sphenodon punctatus*, on Stephens and Lady Alice Islands, New Zealand. *Herpetologica* 44: 25–37.
- Corke, D. 1992: The status and conservation needs of the terrestrial herpetofauna of the Windward Islands (West Indies). *Biological conservation* 62: 47–58.
- Cox, G. 1991: *Prehistoric animals of New Zealand.* Auckland, Harper Collins. 40 p.
- Craig, J. L. 1986: The effects of kiore on other fauna. *In: Wright, A. E.; Beever, R. E. ed. The offshore islands of northern New Zealand. New Zealand Department of Lands and Survey information series* 16: 75–83.
- Cree, A. 1994: Low annual reproductive output in female reptiles from New Zealand. *New Zealand journal of zoology* 21: 351–372.

- Cree, A.; Butler, D. 1993: Tuatara recovery plan (*Sphenodon* spp.). *Threatened species recovery plan series* 9.
- Cree, A.; Daugherty, C. H.; Hay, J. M. in press: Reproduction of a rare reptile, the tuatara *Sphenodon punctatus*, on rat-free and rat-inhabited islands in New Zealand. *Conservation biology*.
- Cree, A.; Daugherty, C. H. 1991: High rates of cutaneous water loss in nocturnal New Zealand reptiles. Unpublished report to Director, Science and Research Directorate, Department of Conservation.
- Crook, I. G. 1973: The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peale). *Proceedings of the New Zealand Ecological Society* 20: 115–120.
- Daugherty, C. H.; Towns, D. R. 1991: The cat's breakfast. *New Zealand science monthly* (April 1991): 13–14.
- Daugherty, C. H.; Towns, D. R.; Atkinson, I. A. E.; Gibbs, G. W. 1990a: The significance of the biological resources of New Zealand islands for ecological restoration. In: Towns, D. R.; Daugherty, C. H.; Atkinson, I. A. E. ed. *Ecological restoration of New Zealand islands. Conservation sciences publication* 2: 9–21.
- Daugherty, C. H.; Cree, A.; Hay, J. M.; Thompson, M. B. 1990b: Neglected taxonomy and continuing extinctions of tuatara (*Sphenodon*). *Nature* 347: 177–179.
- Daugherty, C. H.; Patterson, G. B.; Hitchmough, R. A. 1994: Taxonomic and conservation review of the New Zealand herpetofauna. *New Zealand journal of zoology* 21: 317–323.
- Duggan, E. 1991: Emergence behaviour of *Naultinus gemmeus*, the jewelled gecko, on the Otago Peninsula. *Diploma of Wildlife Management report* 14. University of Otago.
- Fleming, C. A. 1962: The extinction of moas and other animals during the Holocene period. *Notornis* 10: 113–117.
- Freed, L. A.; Conant, S.; Fleischer, R. C. 1987: Evolutionary ecology and radiation of New Zealand birds. *Trends in ecology and evolution* 2: 196–203.
- Gibb, J. A.; Flux, J. E. C. 1973: Mammals. In: Williams, G. R. ed. *The natural history of New Zealand*. Wellington, Reed. Pp. 334–371.
- Green, D. M. 1994: Genetic and cytogenetic diversity in Hochstetter's frog, *Leiopelma hochstetteri*, and its importance for conservation management. *New Zealand journal of zoology* 21: 417–424.
- Hardy, G. S. 1977: The New Zealand Scincidae (Reptilia: Lacertilia); a taxonomic and zoogeographic study. *New Zealand journal of zoology* 4: 221–325.
- Hayman, P. 1984: *Discovering the birds of New Zealand*. Auckland, Collins. 134 p.
- Hicks, G. R. F.; McColl, H. P.; Meads, M. J.; Hardy, G. S.; Roser, R. J. 1975: An ecological reconnaissance of Korapuki Island, Mercury Islands. *Notornis* 22: 195–220.
- Hitchmough, R. A. 1982: The ecology of a population of *Naultinus grayi* Bell near Kaitaia. In: Newman, D. G. ed. *New Zealand herpetology. New Zealand Wildlife Service occasional publication* 2: 399–407.
- Hutton, F. W. 1899: On a supposed rib of the kumi, or ngararu. *Transactions of the New Zealand Institute* 31: 485.
- Janzen, D. H. 1986: Guanacaste National Park: tropical ecological and cultural restoration. San José, Costa Rica, Editorial Universidad Estatal a Distancia.
- Janzen, D. H. 1988: Tropical ecological and biocultural restoration. *Science* 239: 243–244.
- King, C. 1984: Immigrant killers: introduced predators and the conservation of birds in New Zealand. Auckland, Oxford University Press. 224 p.
- King, C. 1990: *The handbook of New Zealand mammals*. Auckland, Oxford University Press. 600 p.
- McFadden, I.; Towns, D. R. 1991: Eradication campaigns against kiore (*Rattus exulans*) on Rurima Rocks and Korapuki Island, northern New Zealand. *Department of Conservation science and research internal report* 97.
- Molloy, J.; Davis, A. 1992: Setting priorities for the conservation of New Zealand's threatened plants and animals. Wellington, Department of Conservation. 44 p.
- Newman, D. G. 1986: Can tuatara and mice co-exist? The status of tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia), on the Whangamata Islands. In: Wright, A. E.; Beaver, R. E. ed. *The offshore islands of northern New Zealand. New Zealand Department of Lands and Survey information series* 16: 175–195.
- Newman, D. G. 1987: Tuatara. Dunedin, McIndoe. 24 p.
- Newman, D. G. 1988: Evidence of predation on a young tuatara, *Sphenodon punctatus*, by kiore, *Rattus exulans*, on Lady Alice Island. *New Zealand journal of zoology* 15: 443–446.
- Newman, D. G. 1994: Effects of mouse, *Mus musculus*, eradication programme and habitat change on lizard populations of Mana Island, New Zealand, with special reference to McGregor's skink, *Cyclodina macgregori*. *New Zealand journal of zoology* 21: 443–456.

- Newman, D. G.; Towns, D. R. 1985: A survey of the herpetofauna of the northern and southern blocks, Great Barrier Island, New Zealand. *Journal of the Royal Society of New Zealand* 15: 279–287.
- Nichol, R. 1988: Tipping the feather against a scale: archaeology from the tail of the fish. Unpublished Ph.D. thesis, lodged in the Library, University of Auckland.
- Parrish, G. R.; Pierce, R. J. 1993: Reptiles of Motuopao Island, Northland, New Zealand. *Tane* 34: 53–58.
- Patterson, G. B. 1992: The ecology of a New Zealand grassland lizard guild. *Journal of the Royal Society of New Zealand* 22: 91–106.
- Patterson, G. B.; Daugherty, C. H. 1990: Four new species and one new subspecies of skinks, genus *Leiopisma* (Reptilia: Lacertilia: Scincidae) from New Zealand. *Journal of the Royal Society of New Zealand* 20: 65–84.
- Pickard, C. R.; Towns, D. R. 1988: Atlas of the amphibians and reptiles of New Zealand. *Conservation sciences publication 1*.
- Robb, J. 1980: New Zealand amphibians and reptiles in colour. Auckland, Collins. 128 p.
- Robb, J.; Rowlands, R. P. V. 1977: Reinstatement of *Hoplodactylus maculatus* (Boulenger) with redescription of *H. pacificus* (Gray) (Reptilia: Squamata: Gekkonidae). *Records of the Auckland Institute and Museum* 14: 133–142.
- Stevens, G.; McGlone, M.; McCulloch, B. 1988: Prehistoric New Zealand. Auckland, Heinemann Reed. 128 p.
- Taylor, R. H.; Thomas, B. W. 1993: Rats eradicated from rugged Breaksea Island (170 ha), Fiordland, New Zealand. *Biological conservation* 65: 191–198.
- Thurley, T.; Bell, B. D. 1994: Habitat distribution and predation on a western population of terrestrial *Leiopelma* (Anura: Leiopelmatidae) in the northern King Country, New Zealand. *New Zealand journal of zoology* 21: 431–436.
- Towns, D. R. 1985: The status and prospects of the rare New Zealand lizards *Leiopisma grande* (Gray), *Cyclodina whitakeri* Hardy and *Leiopisma otagense* McCann (Lacertilia: Scincidae). In: Grigg, G.; Shine, R.; Ehmann, H. ed. *Biology of Australasian frogs and reptiles*. Royal Zoological Society of New South Wales. Pp. 481–489.
- Towns, D. R. 1991: Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: the kiore (*Rattus exulans*). *Journal of the Royal Society of New Zealand* 21: 119–136.
- Towns, D. R. 1992: Recovery plan for Whitaker's skink and robust skink. *Threatened Species Unit recovery plan series 3*.
- Towns, D. R. 1994: The role of ecological restoration in conservation of Whitaker's skink (*Cyclodina whitakeri*), a rare New Zealand lizard (Lacertilia: Scincidae). *New Zealand journal of zoology* 21: 457–471.
- Towns, D. R.; Ballantine, W. J. 1993: Conservation and restoration of New Zealand island ecosystems. *Trends in ecology and evolution* 8: 452–457.
- Towns, D. R.; McFadden, I. 1993: Chevron skink recovery plan *Leiopisma homalonotum*. *Threatened Species recovery plan series 5*.
- Towns, D. R.; Daugherty, C. H.; Newman, D. G. 1985: An overview of the ecological biogeography of the New Zealand lizards (Gekkonidae, Scincidae). In: Grigg, G.; Shine, R.; Ehmann, H. ed. *The biology of Australasian frogs and reptiles*. Royal Zoological Society of New South Wales. Pp. 107–115.
- Towns, D. R.; Atkinson, I. A. E.; Daugherty, C. H. 1990: The potential for ecological restoration in the Mercury Islands. In: Towns, D. R.; Daugherty, C. H.; Atkinson, I. A. E. ed. *Ecological restoration of New Zealand islands*. *Conservation sciences publication 2*: 91–108.
- Towns, D. R.; McFadden, I.; Lovegrove, T. 1993: Offshore islands co-operative project with ICI Crop Care Division: Phase One (Stanley Island). *Department of Conservation science and research internal report 138*.
- Towns, D. R.; McFadden, I.; Thomson, P.; Robertson, H.; Colbourne, R. 1994: Offshore islands co-operative project with ICI Crop Care Division: Phase Two (Red Mercury Island). *Department of Conservation science and research internal report 142*.
- Veitch, C. R.; Bell, B. D. 1990: Eradication of introduced animals from the islands of New Zealand. In: Towns, D. R.; Daugherty, C. H.; Atkinson, I. A. E. ed. *Ecological restoration of New Zealand islands*. *Conservation sciences publication 2*: 137–146.
- Whitaker, A. H. 1973: The lizards of the Poor Knights Islands, New Zealand. *New Zealand journal of science* 11: 623–651.
- Whitaker, A. H. 1978: The effects of rodents on amphibians and reptiles. In: Dingwall, P. R.; Atkinson, I. A. E.; Hay, C. ed. *The ecology and control of rodents in New Zealand nature reserves*. *Department of Lands and Survey information series 4*: 75–86.
- Whitaker, A. H. 1993: The striped skink – a review with recommendations for conservation and management. Unpublished report. Wanganui, New Zealand Department of Conservation.

- Whitaker, A. H.; Loh, G. 1990: A survey of the lizards of the Dunstan Mountains and St Bathans Range area, Otago, 22 February – 3 March 1989. Unpublished report. Dunedin, New Zealand Department of Conservation.
- Williams, G. R. 1973: Birds. *In*: Williams, G. R. *ed.* The natural history of New Zealand. Wellington, Reed. Pp. 304–333.
- Worthy, T. H. 1987a: Osteology of *Leiopelma* (Amphibia: Leiopelmatidae) and descriptions of three new subfossil *Leiopelma* species. *Journal of the Royal Society of New Zealand* 17: 201–251.
- Worthy, T. H. 1987b: Palaeoecological information concerning members of the frog genus *Leiopelma*: Leiopelmatidae in New Zealand. *Journal of the Royal Society of New Zealand* 17: 409–420.
- Worthy, T. H. 1987c: Osteological observation on the larger species of the skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. *New Zealand journal of zoology* 14: 219–229.
- Worthy, T. H. 1991: Fossil skink bones from Northland, New Zealand, and description of a new species of *Cyclodina*, Scincidae. *Journal of the Royal Society of New Zealand* 21: 329–348.