NOVEL PREDATORS AND NAÏVE PREY:

HOW INTRODUCED MAMMALS SHAPE BEHAVIOURS AND POPULATIONS OF NEW ZEALAND LIZARDS

JOANNE MARIE HOARE

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Novel predators and naïve prey: how introduced mammals shape behaviours and populations of New Zealand lizards

Joanne Marie Hoare

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for Olive and friends

Abstract

Biotas that evolved in isolation from mammalian predators are susceptible to degradation due to recent human-mediated introductions of mammals. However, behavioural, morphological and life historical adaptations of prey to novel mammalian predators can allow prey to persist in mammal-invaded areas. Lizards in New Zealand are an ideal group for exploring the effects of invasive mammals on vertebrate prey because: (1) the ca. 80 endemic species evolved without mammals as a major influence for 80 my, (2) mammalian introductions during the past 2000 y have differentially affected lizard species, and (3) some species coexist with mammals on the mainland as well as occurring on mammal-free offshore islands.

I tested three hypotheses: (1) lizard populations that have persisted on New Zealand's mainland are no longer declining in the presence of introduced mammalian predators, (2) introduced mammals induce behavioural shifts in native lizards, and (3) lizard behavioural patterns and chemosensory predator detection abilities vary according to exposure to introduced mammals.

Trends in capture rates of five sympatric native lizard populations over a 23 year (1984-2006) period demonstrate that not all lizard populations that have persisted thus far on New Zealand's mainland have stabilised in numbers. Large, nocturnal and terrestrial species remain highly vulnerable at mainland sites. Introduced kiore, *Rattus exulans*, induce behavioural changes in Duvaucel's geckos, *Hoplodactylus duvaucelii*. A radio telemetric study demonstrated that geckos start reverting to natural use of habitats within six months of kiore eradication. Activity patterns of common geckos, *H. maculatus*, and common skinks, *Oligosoma nigriplantare polychroma*, in laboratory trials are also correlated with their exposure to mammalian predators. Lizard activity (time spent moving) increases relative to freeze behaviour with greater exposure to

mammals. However, specific antipredator behaviours are not elicited by chemical cues of either native (tuatara, *Sphenodon* spp) or introduced (ship rat, *R. rattus*) predators.

Lizard populations may persist by changing their behaviours in the presence of invasive mammals. However, the continued declines of particularly vulnerable mainland lizard taxa suggest that mammal-induced behavioural shifts may only slow population declines rather than enabling long-term survival. Eradicating pest mammals from offshore islands has proven effective at restoring both populations and behaviours of native lizards, but lizard populations on the mainland also deserve conservation priority. Research directed at understanding the synergistic effects of invasive species that are causing continued lizard population declines and mammal-proof fencing to protect the most vulnerable mainland populations from extinction are both urgently required.

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CHAPTER 1

New Zealand lizards as a model to address the influence of novel predators on evolutionarily naïve prey

1.1 Evolution in isolation from mammalian predation pressure

The paradigm of natural selection asserts that differential survival and reproduction of organisms is due to genetic differences among individuals and has driven thinking about evolutionary changes since the late 19th century (Darwin 1859, Endler 1986). Predator-prey interactions are a critical component of natural selection; traits that enable prey to detect and avoid their predators are under strong selection, as are traits that enable predators to detect and capture prey (reviewed by Endler 1986). However, this evolutionary 'arms race' (Van Valen 1973, Dawkins & Krebs 1979) breaks down when either predators or prey are removed from or introduced into a system (Coss 1999, Strauss *et al.* 2006).

'Relaxed selection' occurs when a particular selective pressure, such as a class of predators, is absent from a system. Under relaxed selection characters may disintegrate if mutations that result in loss of a phenotype are not at a selective disadvantage (reviewed by Coss 1999). For example, antipredator characteristics that are costly to maintain may be lost when prey are isolated from a certain class of predators (Coss 1999, Blumstein & Daniel 2005). Comparing behavioural and ecological traits between populations that are either naïve or experienced, in relation to a certain selective agent, can be a powerful tool for investigating patterns of persistence and disintegration of antipredator characteristics (Stone *et al.* 1994, Strauss *et al.* 2006). A system involving reintroduction of a selective agent, after its absence over evolutionary time, can be particularly useful for investigating relaxed selection on antipredator traits and the role experience plays in evoking antipredator responses (Blumstein 2002).

An extreme case of relaxed selection occurred for terrestrial vertebrates in New Zealand and many oceanic islands as a result of their evolutionary isolation from terrestrial mammalian predators (Cassels 1984, Blumstein 2002). Prior to human arrival in New Zealand 2000-1000 years ago (ya; dates are disputed, see Anderson 1996, Holdaway 1996, 1999, Anderson 2000, Hedges 2000), the New Zealand terrestrial fauna evolved in isolation from selective pressures posed by mammalian and snake predators for ca. 80 million years (my)¹. A disproportionate number of birds evolved flightlessness, gigantism prevails in a range of fauna including wētā (large, flightless Orthopterans; Gibbs 1998), geckos (Bauer & Russell 1986), and moa (extinct ratites; Worthy & Holdaway 2002), and many species display K-selected life history strategies with low reproductive outputs (e.g., Cree 1994, Bannock *et al.* 1999, Wilson 2004).

Antipredator traits in New Zealand terrestrial vertebrates evolved in concert with their predominantly visually-oriented avian and reptilian predators, as exemplified by their cryptic colouration and secretive behaviours which reduce predator detection (Worthy & Holdaway 2002). However, many species appear to lack the behaviours necessary to avoid introduced mammalian predators (e.g., Appendix 1) and may in fact be particularly conspicuous to mammals hunting primarily by scent, due to producing strong odours (Worthy & Holdaway 2002). Both the intensity and nature of

¹ Subsequent to submitting this dissertation, the discovery of a nonvolant, mouse-sized mammal from Miocene (19-16 mya) sediments was published (Worthy *et al.* 2006). The finding indicates that evolution of New Zealand biota may have occurred in isolation from land mammals for the last few million years instead of the 80 my since separation of New Zealand from Gondwana as previously presumed.

Worthy, T. H., A. J. D. Tennyson, M. Archer, A. M. Musser, S. J. Hand, C. Jones, B. J. Douglas, J. A. McNamara, and R. M. D. Beck. 2006. Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. *Proceedings of the National Academy of Sciences 103:* 19419-19423.

mammalian predation are likely to be much higher than is sustainable for many of New Zealand's K-selected animal species (e.g., Cree 1994, Moorhouse *et al.* 2003).

1.2 The impacts of invasive species on natives: current knowledge and limitations

Biological invasions can be used to address fundamental ecological and evolutionary questions (Sax *et al.* 2005, Strauss *et al.* 2006). The biogeographic effects of invasive species on native species and populations are reasonably well resolved, at both global and local scales (e.g., Towns & Daugherty 1994, Towns *et al.* 2006). However, the effects of novel selective pressures on individuals are less well known (Losos *et al.* 2004). Life history pattern, morphological and behavioural changes have been observed in of a range of native prey species in response to novel predators (reviewed by Strauss *et al.* 2006). For example, invasive invertebrate predators in North American freshwater streams induce spatial displacement of native water fleas, *Daphnia mendotae*, leading to reduced somatic growth (Pangle & Peacor 2006), shells of the molluscs *Nucella lapillus* increase in thickness following invasion by predatory green crabs, *Carcinas maenas* (Vermeij 1982), and introduced predatory lizards, *Leiocephalus carinatus*, induce spatial displacement in the Bahamian lizards *Anolis sagrei* (Schoener *et al.* 2005).

In New Zealand, both terrestrial and freshwater ecosystems have been drastically altered by exotic predators (mammals and salmonid fish, respectively). Introduced brown trout, *Salmo trutta*, displace native galaxia, *Galaxias vulgaris*, as the principal predators in freshwater streams (McIntosh & Townsend 1994), and induce microhabitat use changes in galaxia (McIntosh *et al.* 1994). Brown trout also influence daily activity patterns of mayflies, *Nesameletus ornatus* (McIntosh & Townsend 1994) and case morphology of caddis flies, *Zelandopsyche ingens* (McIntosh *et al.* 2005), both of which are native prey species. In the terrestrial environment, introduced mammals influence escape responses of arthropods (Bremner *et al.* 1989), daily activity patterns and habitat use of tree wētā, *Hemideina crassidens* (Rufaut & Gibbs 2003), and habitat use of common geckos, *Hoplodactylus maculatus* (Gorman 1996). Studies of individual taxa therefore indicate that novel predators may induce non-lethal effects in native prey species in New Zealand.

1.3 New Zealand lizards as a model system in which to test non-lethal effects of novel predators

The New Zealand lizard fauna comprises ca. 80 endemic species in two orders, the Scincidae and Diplodactylidae (Hickson *et al.* 2000, Han *et al.* 2004, Hitchmough *et al.* in press) and one introduced scincid species (Gill & Whitaker 1996). Although colonisation dates for the endemic lizards are controversial, geckos may be Gondwanan relics (Chambers *et al.* 2001), while skinks are thought to have arrived by ocean rafting 10-25 mya (Daugherty *et al.* 1990b, Hickson *et al.* 2000). The native lizard fauna includes sufficient ecological variety (Gill & Whitaker 1996) and biogeographic patterns (Towns & Daugherty 1994) to act as a model for examining effects of introduced mammals. Many endemic reptiles exhibit relict distributions, as inferred by comparisons of subfossil remains with present-day ranges (Worthy 1987, Towns & Daugherty 1994). A number of larger reptile species, including tuatara, *Sphenodon* spp, the skinks *Cyclodina oliveri*, *C. alani*, *C. macgregori* and *Oligosoma fallai*, and the gecko *H. duvaucelii* are restricted entirely to offshore islands, most of which are free of introduced mammals. Smaller species often persist at mainland (North and South Islands) locations, and some, such as *O. nigriplantare polychroma* and *H. maculatus*,

are both widespread and abundant throughout the mainland where they coexist with a range of mammalian predators (King 2005).

Analysing biogeographic patterns of the reptile fauna has led to hypotheses regarding the relative vulnerability of the endemic lizard taxa to mammals (Whitaker 1978) and facilitated research and conservation prioritising of the most vulnerable species (e.g., Towns 1999, Gaze 2001). Monitoring of lizard population recoveries has been used to assess the effectiveness of current mammal eradication programmes (e.g., Towns 1991, 1996, 2002a). However, the ways in which mammals continue to affect native populations at mainland sites is less well understood (Tocher 2006). Furthermore, although population-level responses of reptiles to rat eradication are well known, individual responses remain poorly researched. The combination of community, population and individual level research into the effect of mammals on native lizards can significantly contribute to understanding of the influences of biological invaders on native species.

1.4 Thesis structure²

In this dissertation, I investigate how endemic lizards in New Zealand, which evolved in the absence of mammals as a selective pressure, are able to persist in the presence of introduced mammalian predators. The New Zealand archipelago, where some islands remain mammal-free with biotas largely representing pre-human New Zealand and others have been invaded to varying degrees by introduced mammals, provides a powerful comparative system for the research (Flannery 1994, Worthy & Holdaway 2002). I test three main hypotheses concerning the relationships between

 $^{^{2}}$ Chapters 2-5 are written as manuscripts. Appendices 1-3 are manuscripts that are relevant, though not essential, to the thesis. Co-authors for publication are listed on the first page of each chapter.

endemic New Zealand lizards and their introduced mammalian predators, which contribute to our understanding of how novel predators influence naïve prey:

- Populations of lizard species that have persisted on New Zealand's mainland are no longer declining in the presence of introduced mammalian predators (Chapter 2).
- 2. Introduced mammals induce behavioural shifts in native reptiles, which facilitate spatial avoidance and hence reptile persistence (Chapter 3).
- New Zealand lizards that evolved in isolation from mammalian predators do not have the antipredator behaviours necessary to avoid mammalian predation.
 Specifically, I investigate behavioural patterns and chemosensory predator detection of lizards with varying experience and evolution with mammals (Chapters 4 & 5).

Firstly, I investigate the hypothesis that lizard species that have persisted on New Zealand's mainland are now numerically stable in the presence of introduced mammalian predators by assessing capture rate trends in a mainland lizard community over the 23 year period 1984 to 2006 (Chapter 2). I take advantage of long-term data from lizard pitfall trapping at a mainland site with sustained mammalian predation (Towns 1985, Towns 1992a, Towns & Elliott 1996). The study encompasses ecological variety (taxonomic affiliation, activity phase, body size and conservation status) among focal taxa, which enables assessment of the relative vulnerability of lizards to habitat modification, disturbance and introduced predators. Analysing and interpreting species-specific trends in the dataset contribute to understanding the current threats to mainland lizard species and allow for reassessment of current management techniques.

Secondly, I test the hypothesis that introduced mammals induce behavioural shifts in native reptiles, by investigating habitat use of New Zealand's largest extant gecko, Duvaucel's gecko, *H. duvaucelii*, in the presence and absence of introduced kiore (Pacific rats, *Rattus exulans*; Chapter 3). By using a 'natural' experiment involving three geographically proximate offshore islands with varying histories of kiore presence and eradication, I explore gecko abundance, population structure and habitat use in relation to kiore. Islands on which geckos were sampled were (1) historically free of all mammals, or from which kiore had been eradicated (2) 20 ya, or (3) 6 mo ago (in which case gecko sampling was also conducted prior to kiore eradication). I also assess habitat use by kiore where they were sympatric with geckos to provide context for among-population comparisons of geckos. The study design enables identification of the temporal lag needed to restore natural behaviours following rat-eradication.

Thirdly, I examine whether isolation from mammalian predators has led to the evolutionary loss of antipredator behaviours, targeting recognition of predator chemical cues. Many squamate reptiles possess highly developed vomeronasal systems and rely on chemical cues to mediate interactions with predators (Schwenk 1993, Cooper 1995a, Schwenk 1995). In the absence of selection from terrestrial mammalian and snake predators, chemosensory antipredator responses in lizard prey may be reduced. An initial investigation of the chemosensory ability of Marlborough green geckos, *Naultinus manukanus*, to detect chemical cues of fruit, conspecifics and native predators (Chapter 4) provides context for a broader investigation of whether native skinks, *O. n. polychroma*, and geckos, *H. maculatus*, use chemoreception to detect and respond to native and introduced predators (Chapter 5). I examine potential variation in this ability according to whether: (1) populations are sympatric or allopatric with mammals, (2) the focal species is common or rare, and (3) the species has an evolutionary history of contact with mammals, in this case using the introduced rainbow skink, *Lampropholis delicata*, as an out-group.

In chapter 6 I synthesise my findings concerning the relationships of endemic New Zealand lizards and their introduced mammalian predators, and the contribution of my

findings to understanding how novel predators influence naïve prey. I discuss conservation implications of investigations of mainland lizard community changes (Chapter 2) and behavioural shifts induced by rodents (Chapter 3), and identify directions for future research.

CHAPTER 2

Long-term monitoring of a lizard guild reveals imminent extinction of the last mainland population of *Cyclodina whitakeri*³

2.1 Abstract

Current primary threats to global biodiversity are species invasions and habitat modification. In New Zealand, introduced mammals are the primary threat to native reptiles. Mammal-free offshore islands provide refugia for many species and have been a focus of conservation. However, many populations of conservation importance occur at mainland sites. I investigate whether lizard populations that have persisted on New Zealand's mainland have attained equilibrium with introduced mammalian predators. The last mainland population of the large, endemic New Zealand skink, Cyclodina whitakeri, and a guild of four sympatric lizard species provide an opportunity to assess lizard population trends at a site affected by invasive mammals and plants. Low abundance of C. whitakeri at the Pukerua Bay Scientific Reserve in the 1980s prompted the removal of grazing stock in 1987 and regular monitoring of the lizard populations by pitfall trapping. Due to low detectability of C. whitakeri, sympatric C. aenea were recommended as an indicator species. Long-term monitoring (1984-2006) of the C. whitakeri population and four other sympatric lizard species within a 336 m² area at the site resulted in 1693 lizard captures over 7597 trap days. The capture rate of Cyclodina whitakeri in 1984-88 was 1.03/100 trap nights, but declined to 0.03/100 trap nights in

³ Co-authors for publication: L.K. Adams, L.S. Bull and D.R. Towns

2000-06 (representing two individuals). Congeneric *C. aenea* showed a similar decline with capture rates also approaching zero by 2006, though capture rates of the diurnal skinks *Oligosoma nigriplantare polychroma* and *O. zelandicum* remained stable, and capture rates of geckos, *Hoplodactylus maculatus*, increased. Removing grazing stock did not result in increased abundance of *C. whitakeri* or *C. aenea*, as intended by management recommendations. Instead, reduced grazing has allowed introduced seeding grasses to proliferate, which may have led to periodic rodent irruptions, supporting a guild of introduced mammalian predators and depleting populations of *C. whitakeri* and *C. aenea*. Thus, despite coexisting with introduced mammals for at least 1000 years, some mainland lizard populations continue to decline, even when conservation strategies are in place.

2.2 Introduction

Conservation of vulnerable species relies heavily upon research identifying threats and effective management (Caughley 1994). Habitat modification and introductions of invasive species are key threats to native biodiversity on a global scale (e.g., Case & Bolger 1991, Sinclair *et al.* 1998). In archipelagos, the most vulnerable native fauna often become restricted to outlying islets, where anthropogenic threats are absent or reduced; such islets have naturally become targets for effective conservation (e.g., Worthy 1987, Daugherty *et al.* 1990a, Towns & Ballantine 1993). Protecting species at mainland sites where introduced predators cannot be completely excluded presents a greater challenge, yet is necessary where certain habitats (Tocher 2006) or species assemblages (Towns & Elliott 1996) are present only on the mainland. The last remaining mainland population of a large skink, *Cyclodina whitakeri* (Whitaker's skink), coexists with four other endemic lizard populations and provides an opportunity to investigate whether (1) New Zealand lizard populations have reached an equilibrium with introduced mammalian predators at mainland sites, and (2) current conservation practices are effective at protecting vulnerable mainland populations.

Cyclodina whitakeri are classified as 'vulnerable' by the World Conservation Union due to acute range restriction and small population sizes (IUCN 2006). The last mainland population, at Pukerua Bay, represents one of only three remaining natural populations; the other two exist on mammal-free offshore islands in north-eastern New Zealand (Middle and Castle Islands). Furthermore, preliminary evidence based on microsatellite markers suggests that the Pukerua Bay *C. whitakeri* population is genetically distinct from the two northern populations (K. Miller, unpubl. data). The relic distribution of *C. whitakeri* (Worthy 1987) is indicative of vulnerability to the effects of both introduced predatory mammals and habitat modification, which afflict many New Zealand species, including lizards (Daugherty et al. 1993). *Cyclodina whitakeri* may be particularly prone to these effects due to its relatively large body size, long life span, low reproductive output, precise temperature requirements and nocturnal habit (Cree & Daugherty 1991, Towns 1994, Gill & Whitaker 1996, Towns 1999).

Due to the conservation importance of the Pukerua Bay *C. whitakeri* population, a pitfall trapping study was conducted between 1982 and 1988 to identify threats to population persistence and recommend management solutions (Towns 1992a, Towns & Elliott 1996). During this period, *C. whitakeri* were the least abundant lizard of five species present at the site, representing 2.7% of all captures (Towns & Elliott 1996). As they showed a preference for stony substrates with little subsurface liane, a management strategy involving revegetation to support increased habitat availability was embarked upon (Towns & Elliott 1996). By removing grazing stock from the reserve, it was hoped that quantity and quality of habitat available to *C. whitakeri* would increase. Simultaneous revegetation was also recommended to limit the extent of introduced

seeding grasses, which would passively control the abundance of mice (mouse populations irrupt following seeding events; Fitzgerald et al. 2004) and other introduced predatory mammals. As *C. whitakeri* were in low numbers and difficult to detect, it was recommended that congeneric *C. aenea* (copper skink) be used as an indicator species to assess the effectiveness of management through an ongoing monitoring programme (Towns & Elliott 1996).

In 1987, a fence was constructed to exclude stock from the site, but only natural revegetation occurred. Therefore, active management involved removal of grazing stock without revegetation, which raises other potential threats to the lizard populations. If rank grasses were allowed to proliferate, potential threats included risks from fire and possible irruptions of mice and their predators, such as cats and mustelids, which all prey on lizards. Pitfall trapping for lizards continued at the site from 1991 to the present. Such monitoring allows analysis and discussion of capture rate trends not only for the nocturnal *C. whitakeri* population, but also for an assemblage of more common sympatric lizard species: congeneric, crepuscular *C. aenea*, the diurnal skinks *Oligosoma nigriplantare polychroma* (common skink) and *O. zelandicum* (brown skink), and the nocturnal gecko *Hoplodactylus maculatus* (common gecko). Furthermore, I resurveyed habitat at the site 20 years after the initial study to assess effects of grazing stock removal and investigated the presence, abundance and diet of rodents and mustelids at the site in 1998.

I assess long-term (23 year) trends in capture rates of the Pukerua Bay lizard assemblage in the context of habitat changes and mammal abundance to evaluate the following alternate hypotheses raised by Towns and Elliott (1996) for a management scenario involving removal of grazing stock but no revegetation:

1. Protection of habitat against stock improves the quality and quantity of available habitat, such that species sensitive to predation and disturbance (in this case, *C*.

whitakeri, C. aenea and *H. maculatus*) show an increasing trend in capture frequency over time;

2. Reduced grazing increases the extent of introduced seeding grasses leading to periodic irruptions of rodents and increased detrimental effects of these and other introduced predatory mammals. In this case, *C. whitakeri*, and perhaps other lizard species decline in capture frequency.

2.3 Methods

2.3.1 Study site and species

The 12.3 ha Pukerua Bay Scientific Reserve is located on north-facing slopes above a rocky beach on the south-west coast of the North Island of New Zealand. The reserve has a history of recurring fires and grazing of stock, which has maintained vegetation at an early successional stage. Removal of grazing animals and fencing of the reserve (1987) and feral goat control (1998 onwards) facilitated partial restoration of coastal forest in gullies, but may have allowed weeds to proliferate. A complex array of boulders and regenerating scrub provides habitat for five lizard species (Towns & Elliott 1996), including nocturnal and diurnal species that exhibit differing life history characteristics and a range of habitat requirements (Table 1). The main predators of these lizard species are native and introduced birds (e.g., Whitaker 1972, Fitzgerald *et al.* 1986, Bell 1996), and introduced mammals (reviewed in Table 2).

The reserve has a history of irregular mammal indexing and control. Rodent control occurred in 1995 (Miskelly 1997), and control of both rodents and mustelids was conducted in 1998, 1999 and 2004-06. Rodents were poisoned using an

Table 1. Morphometric, reproductive and ecological information for all lizard species found at Pukerua Bay, North Island, New Zealand. SVL stands

 for snout-vent length. * Mean litter size varies on a latitudinal gradient, therefore values given are for the Wellington region

Species	Maximum SVL	Activity	Habitat proformance	Status	Age at sexual	Mean litter
Species	(mm)	phase	nabitat preference	Status	maturity	size*
Cyclodina aenea	62 ^a	Diurnal/ crepuscular ^{a,b,c}	Generalist ^d	Widespread ^d	2-3 y ^e	2.17 ^{f,g}
C. whitakeri	101 ^a	Nocturnal/ crepuscular ^a	Coastal forest & vegetated boulder bank ^a	Vulnerable ^h	4 y ⁱ	1.5 ^j
Hoplodactylus maculatus	82 ^a	Nocturnal, but sun basks ^a	Generalist ^a	Widespread ^a	4 y ^k	1.98 ^g
Oligosoma nigriplantare polychroma	77 ^a	Diurnal ^{a,b}	Generalist ^a	Widespread ^a	Unknown	5.13 ^{f,g}
O. zelandicum	73 ^a	Diurnal ^{a,b}	Moist and shaded locations ^{a,1}	Locally abundant ^a	Unknown	5.29 ^m

Information from: ^aGill & Whitaker 1996, ^bHare et al. 2006, ^cPorter 1987, ^dPickard & Towns 1988, ^eTowns 1991, ^fas *Leiolopisma zelandica* Barwick 1959, ^gCree 1994, ^hIUCN 2006, ⁱTowns 1994, ^jTowns 1992b, ^kWhitaker 1982, ^lTowns & Elliott 1996, ^mGill 1976.

Introduced mam	mal	Lizard species as prey ^a	Site	Reference(s)
House mice	Mus musculus	Cyclodina aenea	PB; Mana Is.	Towns 1992a ^b ; Newman 1994 ^b
		C. whitakeri	PB	Towns 1992a ^b
		Hoplodactylus maculatus	PB; Mana Is.	Towns 1992a ^b ; Newman 1994 ^{b,c}
		Oligosoma nigriplantare polychroma	PB; Mana Is.	Towns 1992a ^b ; Newman 1994 ^b
		O. zelandicum	PB; Mana Is.	Towns 1992a ^b ; Miskelly 1999 ^c
Ship rat	Rattus rattus	H. maculatus	PB	this study
Weasel	Mustela nivalis	C. whitakeri	PB	Miskelly 1997
		O. zelandicum	PB	Miskelly 1997
Stoat	Mustela erminea	O. n. polychroma	Kaikoura Range	Cuthbert et al. 2000 ^e
Cat ^d	Felis catus	C. aenea	Auckland	Gillies & Clout 2003
		O. n. polychroma	Otago	Norbury 2001
Hedgehog	Erinaceus	H. maculatus	Waitaki	Jones et al. 2005 ^{e,f}
	europaeus	O. n. polychroma	Waitaki	Jones et al. 2005

Table 2. Introduced mammals present at the Pukerua Bay (PB) Scientific Reserve (from Miskelly 1997, Tuohy 2005, L. Bull, unpubl. data), and

evidence (from PB and elsewhere in New Zealand) for predation on the five lizard species present at the site.

^aOnly lizard species known to occur at the Pukerua Bay Scientific Reserve are included; ^bKilled in pitfall traps during monitoring; ^cIndirect evidence from pre- and post-eradication monitoring; ^dNot recorded in traps at the Pukerua Bay Scientific Reserve, but likely to be present, as cats are abundant in the nearby township (250 m distant); ^eRemains not identified to species level, but species inferred from local distribution and abundance; ^fUnder taxonomic revision, but affiliated with the *H. maculatus* species complex (Hitchmough 1997)

anticoagulant toxin or trapped using peanut butter and rolled oats as a lure. Mustelids were trapped using hen eggs as a lure. Weasels (*Mustela nivalis*), stoats (*M. erminea*), ship rats (*Rattus rattus*), house mice (*Mus musculus*), and hedgehogs (*Erinaceus europaeus*), have been captured at the site (Miskelly 1997, Tuohy 2005, this study). Cats (*Felis catus*) are also doubtless present, as there is a township only 250 m distant from the site (Towns 1999). I review evidence from both Pukerua Bay and elsewhere in New Zealand of predation by these mammals on the focal lizard taxa (Table 2) and present information on stomach contents of mammals caught in 1998 (see below).

2.3.2 Lizard trapping

The core habitat for *C. whitakeri* at Pukerua Bay is a 336m² bank of greywacke boulders, bound by native liane Muehlenbeckia complexa (pohuehue; Towns & Elliott 1996) and has been the focal area for lizard trapping throughout the study (1984-2006). Exploratory pitfall trapping for lizards commenced at the Pukerua Bay Scientific Reserve in December 1982. Captures of 2,897 lizards over 23,667 trap days in a 720 m^2 grid between then and March 1988 were discussed by Towns (1985), Towns (1992b) and Towns and Elliott (1996). I re-analyse captures from 336 m^2 of the grid to investigate long-term lizard population trends in this paper. Low intensity monitoring by means of pitfall trapping was continued at this 336 m² site between 1991 and 1997 by the Department of Conservation (DoC), primarily to detect the continued presence of the C. whitakeri population. Data from years in which traps were only opened once (1992 and 1993) were excluded from graphs, but all trapping sessions were included in statistical analyses. Pitfall trapping effort by the DoC intensified from 1998 onwards, due to concerns over the persistence of C. whitakeri, following low capture rates between 1991 and 1997 (Table 3). In January-March, between 1984 and 2006, 1693 lizards were captured over 7597 trap nights over the 336 m^2 site (Table 3). I use these

Table 3. Lizard pitfall trapping effort and captures at a 336 m² core site at PukeruaBay, North Island, New Zealand 1984-2006. 'Trap nights' is trapping effort calculatedas the sum of the number of days each trap was open during each January-March period.Traps were open for 24-96 h in 1984-95 and only 24 h thereafter.

		Number of lizard captures						
	Trap	Cyclodina	С.	Hoplodactylus	Oligosoma	0.		
Year	nights	aenea	whitakeri	maculatus	nigriplantare polychroma	zelandicum		
1001	250	26	2	11	10	21		
1984	239	20	3	11	48	21		
1985	333	11	2	3	38	3		
1986	259	39	1	4	24	12		
1987	222	49	6	1	97	31		
1988	185	9	1	1	23	2		
1989	0							
1990	0							
1991	36	3	2	0	0 13			
1992	18	0	0	0 5		1		
1993	18	3	1	0	11	1		
1994	54	2	1	0	11	1		
1995	107	3	0	1	36	1		
1996	162	4	1	9	51	5		
1997	150	2	0	6	13	3		
1998	0							
1999	0							
2000	286	13	0	8	115	20		
2001	479	3	1	13	103	9		
2002	1596	10	0	51	28	15		
2003	0							
2004	1679	0	0	44	64	23		
2005	1099	6	1	202	69	37		
2006	655	0	0	39	131	29		
Total	7597	183	20	393	880	217		

captures as the basis for analyses of long-term population trends in the Pukerua Bay lizard assemblage.

Lizard capture frequencies were assessed by pitfall trapping using 4 L tin or plastic containers (hereafter referred to as traps) dug into the ground at 2-4 m intervals. The more durable plastic containers were introduced in 1991. Traps were covered to provide shade and minimise the risk of predation and a damp sponge was place in each trap to prevent desiccation of lizards. Canned pear was placed in each trap to attract lizards, set for 24-96 h prior to 1997 and 24 h thereafter (in accordance with tightening ethical regulations), and checked for lizards starting at ca. 0900 h (NZDT).

2.3.3 Weather data

I obtained weather data for each trapping period from the National Climate Database (NIWA 2006). I used the weather station at Paraparaumu airport, which is the nearest mainland weather station to the Pukerua Bay study site (17 km distant) with records throughout the trapping period (1984-2006). I obtained information on maximum and minimum air temperature, rainfall and sunshine hours for each 24 hour period that traps were open. Where traps were open for more than 24 hours (1984-95), I took an average for each weather variable across days that traps were open. Additionally, I obtained mean annual data (1984-2005) for each variable from the same weather station, to assess potential trends.

2.3.4 Habitat sampling

Habitat in the 336 m² trapping grid was surveyed in September-October 1986 (see Towns & Elliott 1996) and I resurveyed it in June 2006 using the same methodology, to investigate any long term changes. At each 4 m interval within the grid, 25 measurements of both vegetation and substrate were made every 0.25 m over a 1 m²

area (i.e., N = 800 measurements in each year). Measurements taken at each sampling point were vegetation height, species composition (first species encountered from above sampling point), and substrate composition at and beneath the surface. Substrates were classified as loam (loam, clay, silt, sand and gravel; particle size <0.06 m), stones (0.06-0.20 m), boulders (>0.21 m), wood and creeping vegetation. Die-back of perennial plants, notably the prevalent, introduced *Lathyrus latifolius* (everlasting pea), was accounted for in June 2006 (winter) by including dead plants in vegetation height and composition measurements.

2.3.5 Mammal trapping and stomach content analyses

Fifty permanent rodent index trap sites were established by Leigh Bull at 25 m intervals adjacent to the core *C. whitakeri* site at Pukerua Bay. At each of these sites a pair of rat and mouse snap traps baited with a mixture of peanut butter and rolled oats were set and checked over three consecutive trap nights in January, March, April, May, June and August 1998. During the same period Fenn trap boxes, each containing two Fenn traps targeting mustelids, were placed at ca. 150 m intervals near rodent trap sites. The study included nine Fenn trap boxes from January until May (inclusive) and eight trap boxes thereafter. Each box was baited with a single pierced hen egg placed between the two traps and checked over three consecutive days.

All mammals caught were identified to species level. Stomach contents were removed, shaken vigorously in warm water and passed through a 0.5 mm sieve for identification under a binocular microscope. Evidence of bait consumption was disregarded.

2.3.6 Statistical analyses

As pitfall traps were set for 24-96 h prior to 1997, and for 24 h thereafter, I needed to account for skinks that would have been caught in consecutive trap days had traps been checked daily throughout the study. I fitted a species-specific exponential curve based on number of lizards captured when traps were set for 24, 48, 72 or 96 h between 1984 and 1988 at Pukerua Bay (data from Towns & Elliott 1996), and solved for a standard 24 h trapping period. In this way I obtained one capture estimate per trapping period using the equation:

$$y = N * (1 - e^{-\lambda d})$$

where y is predicted captures if traps were open for 24 h, N is number of lizards caught in d trap days and λ is the rate of increase in captures. No correction factor was applied to geckos, as they are able to climb out of pitfall traps (pers. obs.), and hence gecko captures are likely to reflect only the previous 24 h of trapping.

I assessed the influence of both biological variables and trends across time on capture rates of each lizard species at Pukerua Bay using univariate analyses of variance (ANOVAs) in the statistical programme 'R' (version 1.9.1; R Development Core Team, 2004). The trapping session was used as the unit of replication. Capture rate (captures per 100 trap nights) was the dependent variable, and combinations of time (year), maximum and minimum air temperature, rainfall and sunshine hours were included as factors. Akaike's Information Criteria (AIC) were used in statistical model selection to assess the combination of factors that best predicted capture rate (see Burnham & Anderson 1998).

Potential temporal trends in weather variables over the 23 year period of the study were also assessed using univariate ANOVAs in 'R'. In separate analyses, each weather variable was the dependent variable and time (year) was included as a fixed factor.

2.4 Results

All five lizard species at Pukerua Bay showed high variability in capture rate during the 23 year period 1984-2006 (Fig. 1), yet trends within each species were discernable. Both *C. aenea* (crepuscular) and *C. whitakeri* (nocturnal) decreased in capture frequency during this period (t = -12.20, p < 0.001 and t = -5.388, p < 0.001, respectively) to approach zero (Fig. 1a & b). The already low capture frequency of the least abundant species at the site, *C. whitakeri*, declined from 1.03/100 trap nights in the period 1984-88 to 0.03/100 trap nights in the period 2000-06, representing a 34-fold decrease in capture frequency. Meanwhile, capture rates of the indicator species, *C. aenea*, declined from 11/100 trap nights to 0.55/100 trap nights, representing a 20-fold decrease. Capture rates of diurnal, *O. n. polychroma* and *O. zelandicum* fluctuated substantially on an annual basis, but showed no linear trend (p > 0.05 for both; Fig. 1d & e). In contrast, capture rates of nocturnal geckos, *H. maculatus*, increased during the same period (t = 3.988, p < 0.001; Fig. 1c).

In addition to temporal trends in lizard capture frequencies, local weather during the period that traps were open was related to capture rates of some species (Table 4). Maximum air temperature was positively related to captures of *C. aenea* (t = 12.305, *p* < 0.001) and *O. zelandicum* (t = 2.946, *p* = 0.004; Table 4). Captures of *H. maculatus* generally increased with temperature (t = -4.140, *p* = 0.004; Table 4), though an interaction with time was driven by unusually high capture rates in 2005 (Fig. 1c) coinciding with high maximum temperatures. Captures of *O. n. polychroma* were negatively related to rainfall (t = -2.469, *p* = 0.014; Table 4). I found no temporal trends in mean annual weather variables over the 22 year period 1984-2005 (p > 0.5 for all).





Figure 1. Capture frequencies (mean \pm SE), per 100 trap nights, of all lizard species found at a 336 m² site at the Pukerua Bay Scientific Reserve, North Island, New Zealand between 1984 and 2006. Capture frequencies of (a) *Cyclodina aenea* and (b) *C. whitakeri* declined (p < 0.001 for both). However, capture rates of (c) *Hoplodactylus maculatus* increased (p < 0.001), and populations of both (d) *Oligosoma nigriplantare polychroma* and (e) *O. zelandicum* remained stable (p = 0.241 and p = 0.651, respectively). Significant linear trends are indicated by dashed lines.



Table 4. Results of statistical analyses investigating factors influencing capture rate trends in lizards at Pukerua Bay 1984-2006. Combinations of time (year), maximum (Tmax) and minimum air temperature, rainfall (rain) and sunshine hours were assessed for predictive powers using Akaike's Information Criteria. An asterisk (*) indicates an interaction term.

Species	Best model	Factor(s)	t	р
Cyclodina aenea	Tmax + Year * Tmax	Tmax	12.305	< 0.001
		Year * Tmax	-12.177	< 0.001
C. whitakeri	Year	Year	-5.388	< 0.001
Hoplodactylus maculatus	Year + Tmax + Year $*$ Tmax ^a	Year	-3.608	< 0.001
		Tmax	-4.140	< 0.001
		Year * Tmax	4.162	< 0.001
Oligosoma nigriplantare polychroma	Rain	Rain	-2.469	0.014
O. zelandicum	Tmax	Tmax	2.948	0.004

^a These results are driven by the 2005 outlier (see Fig 1c). Excluding these data the best model becomes Year + Tmax; capture rates increase with both time (year) and maximum temperature (t = 3.620, p < 0.001 and t = 2.902, p = 0.004, respectively).

A comparison of relative lizard capture frequencies during the period 1984-2006 (Table 5) supports the trends seen within each species (Fig. 1). *Cyclodina whitakeri* represented 2.8% of total captures in 1984-88, but declined relative to other species to represent only 0.2% of all captures in 2000-06. In a similar decline, the proportion of captures of *C. aenea* was reduced from 28.8% in 1984-88 to 2.6% in 2000-06 (Table 5). The frequency of diurnal skink *O. n. polychroma* and *O. zelandicum* encounters remained relatively steady, whereas the gecko *H. maculatus* increased from 4.3% to 29.1% of total captures. Excluding geckos from calculations does not alter the trends seen in relative capture rates of skinks (Table 5).

Although substrate and vegetation composition at the Pukerua Bay lizard trapping site were generally similar in 2006 to those recorded in 1986, subtle changes did occur (Table 6). The greatest substrate change was an increase in surface (from 0% to 4.13%) and subsurface (from 1.10% to 11.00%) creeping vegetation between 1986 and 2006. Proportions of other substrate types were similar, though a greater proportion of loam relative to stones was found in the subsurface in 2006. Entangled Coprosma propingua and *M. complexa* are the most frequently encountered vegetative species (76.26% and 72.01% in 1986 and 2006, respectively; Table 6). Other vegetation at the site is mostly comprised of adventive, early successional species, particularly grasses (see Towns 1992a for a species list). In 1986, 11.50% of ground had no vegetative cover; adventive species encroached to reduce exposed areas to 3.63% of the site in 2006 (Table 6). In particular, introduced *Ehrhata erecta* (veld grass), which was present in the Pukerua Bay Scientific Reserve in 1986 (but not in the core lizard monitoring site; Towns 1992a), increased in cover to become the spatially dominant adventive species in 2006 (58% of adventive species). However, mean vegetation height remained unchanged in the 20 year period 1986-2006 (0.39 m in 1986 and 0.41 m in 2006; Table 6).

Table 5. Species composition of lizards at a 336 m^2 site at the Pukerua Bay Scientific Reserve, North Island, New Zealand in 1984-88, 1991-97 and2000-06.

	1984-88			1991-97			2000-06		
Species	Captures	Captures Percentag		Captures	Percentage of total		Captures	Percentage of total	
		All	Skinks		All	Skinks		All	Skinks
		lizards	only		lizards	only		lizards	only
Cyclodina aenea	134	28.8	30.0	17	8.8	9.6	32	3.1	4.7
C. whitakeri	13	2.8	2.9	5	2.6	2.8	2	0.2	0.3
Hoplodactylus maculatus	20	4.3	-	16	8.3	-	357	34.5	-
Oligosoma nigriplantare	230	49.3	51.6	140	72.5	79.1	510	49.3	75.3
polychroma									
O. zelandicum	69	14.8	15.5	15	7.8	8.5	133	12.9	19.6
TOTAL	466	100	100	193	100	100	1034	100	100

Table 6. Comparison of habitat at a 336 m^2 site in the Pukerua Bay Scientific Reservein 1986 versus 2006. Substrate size classes are: boulder (> 0.21 m), stone (0.06-0.20 m)and loam (< 0.06 m).</td>

	Habitat		1986	2006
Туре	Category		N = 800	N = 800
SUBSTRATE				
Surface (% covered)	Boulder		13.58	11.25
	Stone		56.73	53.00
	Loam		28.55	28.13
	Wood		1.13	3.50
	Creeping vegetation		0	4.13
Subsurface (% covered)	Boulder		1.75	3.75
	Stone		59.25	38.00
	Loam		37.88	46.75
	Wood		0.13	0.50
	Creeping vegetation		1.00	11.00
VEGETATION				
Mean height (m)			0.39	0.41
Species (% covered)	Coprosma propinqua	Shrub	11.63	25.88
	Muehlenbeckia complexa	Liane	64.63	46.13
	Adventive plants		5.53	23.02
	None		11.50	3.63
	Other native species		6.71	0.93
Rodents were caught in all trapping sessions between January and August 1998. On average (median), 20.1 house mice and 1.7 ship rats were caught per 100 trap nights. Captures of both house mice (N = 304) and ship rats (N = 15) peaked in March (34.7 and 5.2 per 100 trap nights, respectively). Stomach content analyses revealed that both rats and mice consume primarily invertebrate and plant material. However, one mouse stomach contained remains of an unidentifiable skink, and three rats (i.e., 20% of rats) had consumed geckos, *H. maculatus*. During the six trapping periods, only one mustelid, an adult male stoat, was captured (in the August trapping session). No animal remains were detected in the stoat's stomach or gut.

2.5 Discussion

I provide strong evidence that the lizard community at Pukerua Bay, a species-rich mainland site on New Zealand's North Island, is rapidly changing. Capture rates of focal, large nocturnal skinks, *C. whitakeri*, declined dramatically over the 23 year period 1984-2006. Surprisingly, the same trend in capture frequency was seen for smaller, crepuscular *C. aenea* which were recommended as an indicator taxon to monitor effectiveness of management (Towns & Elliott 1996). In contrast, capture rates of the diurnal skinks *O. n. polychroma* and *O. zelandicum*, remained stable and those of nocturnal geckos, *H. maculatus*, apparently increased. However, I cannot exclude the possibility that increased capture frequencies of geckos represent a response to a change of trap type and shortened trap clearance times. I cannot accept the hypothesis that protection of the site from stock has increased its capacity to support *C. whitakeri* (Towns & Elliott 1996). Instead, I provide support for the hypothesis that decreased grazing increases the extent of introduced grasses, which may lead to periodic irruptions of rodents and increased predation of *C. whitakeri* and *C. aenea* by mammals.

Increasing evidence suggests that threats to biodiversity may interact (e.g., Courchamp *et al.* 1999a, 1999b, Norbury 2001) such that modifying one agent of decline may not improve the prospects of a native population, and may even make matters worse.

2.5.1 Synergistic effects of habitat changes and introduced predators on mainland lizard populations

A managed revegetation programme was recommended to conserve the small *C. whitakeri* population remaining at Pukerua Bay following a study in the 1980s (Towns 1992a, Towns & Elliott 1996). Management recommendations were followed in part; grazing stock were removed, but replanting did not occur. Under this scenario, Towns (1992a) predicted the rapid spread of rank grass and other weeds, an increase in binding vegetation on scree and gradual improvement of forest remnants. I find support for an increase in the extent of grass, weeds and binding vegetation but no evidence as yet for the enhancement of forest remnants. Based on these habitat changes, Towns (1992a) predicted a reduction in numbers of *O. n. polychroma*, due to vegetation covering the open areas that they commonly inhabited, and an increase in numbers of *C. aenea* and *O. zelandicum* associated with greater binding vegetation on scree. Neither prediction eventuated; instead *O. n. polychroma* and *O. zelandicum* populations remained stable and *C. aenea* declined dramatically.

The 34-fold decline in large, nocturnal skinks, *C. whitakeri*, and 20-fold decline in crepuscular skinks, *C. aenea*, were not predicted as species-specific outcomes of the management regime that eventuated (Towns 1992a, Towns & Elliott 1996). I propose two mechanisms that may be responsible for declines seen in the two *Cyclodina* species: (1) increased rank grass associated with removal of grazing stock supports irruptions of rodents and their mustelid and cat predators, which also prey on lizards, and (2) increased subsurface binding vegetation decreased interstitial spaces between substrate

particles and limits lizards' access to refugia that afford protection from introduced predators. Synergism between subtle habitat changes and sustained mammalian predation pressure is likely to disproportionately affect species with relatively large body sizes, and/or a nocturnal or crepuscular activity phase which is shared by many predatory mammals (Whitaker 1978, Daugherty *et al.* 1993, Towns & Daugherty 1994).

Mammalian predation pressure on lizards at Pukerua Bay is likely to have intensified after stock were removed, due to the spread of introduced grasses resulting in increased population fluctuations of both rodents and their mammalian predators (as predicted by Towns & Elliott 1996). Mammalian predation rates may have reached a level where they threatened population persistence of particularly vulnerable species. A similar mechanism drives mammalian predation intensity at a lizard-rich South Island site, though in this instance predation is linked to density of European rabbits, Oryctolagus cuniculus cuniculus, as the primary prey (Norbury 2001). That fluctuations of rodent populations could drive the Pukerua Bay faunal community is supported by evidence of substantial lizard population responses to mouse eradication on nearby Mana Island (Newman 1994). Though no data on rodent densities prior to the removal of grazing stock are available, data spanning eight months in 1998 show increases in both rat and mouse capture rates at the end of summer. Low rates of lizard predation by mammals detected in 1998 are unlikely to accurately reflect populationlevel effects of mammalian predation, due to limitations associated with stomach content analyses (Towns et al. 2006). Use of bait is likely to be particularly attractive to hungry mammals and destructive sampling results in a snapshot of diet at a single point in time for each mammal trapped (reviewed by Towns et al. 2006). Evidence from other mainland New Zealand sites with high lizard abundance suggests that mammalian predation rates are particularly significant due to their extreme variability and intensity (Norbury 2001). For example, nineteen skinks were found in a single ferret (*M. furo*)

scat (Norbury 2001), 35 skinks were found in one feral cat scat (Norbury 2001), and skinks occurred in 61 of 788 stoat scats (Cuthbert *et al.* 2000).

2.5.2 Conservation management of herpetofauna at disturbed sites

Recent conservation advances in New Zealand have been achieved through comprehensive control of introduced mammals threatening native species at mainland sites (Saunders & Norton 2001, Lovegrove *et al.* 2002). A variety of 'mainland islands', which are isolated from the rest of the mainland by intensive predator control, act as sanctuaries for threatened native biotic communities, particularly of birds. However, there is little evidence that this practice has been of benefit to resident lizards. Instead, current management practices directed at recovery of threatened lizard taxa on mainland New Zealand appear to be alarmingly ineffective.

The regional conservation management strategy, which guides management of Pukerua Bay and its lizard assemblage, places emphasis on the need to protect the habitat and population of *C. whitakeri* at this last mainland site (New Zealand Department of Conservation 1996). In light of the removal of grazing animals from core lizard habitat at Pukerua Bay actually having detrimental effects on the target *C. whitakeri* population, there are four options that must be considered: (1) no management; (2) releasing stock back into the reserve; (3) continued concurrent mammal control and lizard trapping to remove any *C. whitakeri* individuals for translocation to a mammal-free offshore island, and (4) construction of a predator-proof fence around the core *C. whitakeri* habitat to allow for either *in situ* conservation or translocation following population recovery. Each option is discussed in more detail:

(1) **No management:** The *C. whitakeri* population is barely detectable. It is possible that pitfall trapping does not accurately reflect population size of *C. whitakeri*, which may be semi-fossorial (A. Whitaker, pers. comm.), though the long-term decline

in capture rates using consistent methodology clearly indicates a population trend and a critically low population size is probable. In the last 5794 trap days, spanning seven years, only two individual *C. whitakeri* (both male, one sub-adult) have been captured. Both skinks have been taken into captivity (D. Keall, pers. comm.) with the intention of establishing a captive population for translocation to a mammal-free offshore island (Miskelly 1999, Towns 1999). Their presence indicates that a very small population persists at the site, presumably using deep screes as refugia. Without immediate management intervention it is likely that the population will not survive. However, the management effort required to procure two individuals was enormous, mammal control has not produced a measurable response in lizard populations, and it may be time to direct conservation funds elsewhere.

(2) **Releasing stock back into the reserve:** I provide some evidence that the removal of grazing stock has triggered a complex response among introduced species at Pukerua Bay, which has ultimately been detrimental to the *C. whitakeri* population. However, releasing grazing stock back into the Reserve is a risky move, as it is likely to curb the natural revegetation process that may be beneficial to the lizard assemblage in the long-term (Towns 1992a), and it is unlikely to afford sufficient protection from mammalian predation to allow recovery of the *C. whitakeri* population. Previously, management recommendations were based on a small, but stable *C. whitakeri* population, in which case gradual improvement was managed for (Towns 1992a); management must now be based on very a very low population size and the need for rapid recovery.

(3) **Mammal control and** *C. whitakeri* salvage: Mammal control at mainland sites elsewhere in New Zealand has enabled survival of a range of vulnerable species (e.g., Saunders & Norton 2001, Lovegrove *et al.* 2002, Spurr *et al.* 2005). Effects of mammal control on lizard populations at the Pukerua Bay Scientific Reserve conducted in 2004-06 may only be detected after a considerable lag time, due to slow response times of long-lived lizards (Cree 1994, Towns 2002b). Therefore, the current option of simultaneous mammal control and lizard salvage may eventually procure sufficient *C*. *whitakeri* individuals to translocate to nearby mammal-free Mana Island in the hope of establishing a self-sustaining population (Miskelly 1999, Towns 1999). However, in a parallel mainland situation, declines of the South Island species *Oligosoma grande* and *O. otagense* have continued despite the control of introduced predators (Tocher 2006). Results from the past seven years suggest that even salvage of sufficient *C. whitakeri* individuals through continued pitfall trapping and simultaneous mammal control is no longer a viable option.

(4) **Mammal-proof fence:** Construction of predator-proof fences is the most recent and effective measure to protect mainland populations from introduced mammalian predators. The area occupied by *C. whitakeri* at Pukerua Bay may be suited to this approach because of its restricted extent (ca. 1 ha). Such intervention is likely to offer the best chance of rescuing the highly threatened *C. whitakeri* population from local extinction or, at the very least, protecting sufficient numbers in the short term to act as a reservoir for translocating to a more secure site offshore. However, it does present a number of challenges which include: high start-up costs, the difficulty of constructing a fence at a coastal site with deep screes, permanently excluding mice and drawing public attention to *C. whitakeri* habitat. The possibility that numbers of remaining *C. whitakeri* at the site are too low to show a population-level response to management must be considered.

Ultimately, the value judgement over which management option to proceed with should be based upon consultation with all stakeholders. The population now persists at such low density that procuring enough individuals to protect a self-sustaining population, either *in situ* or even on a mammal-free offshore island, would be a

remarkable achievement. If protecting this last mainland population of *C. whitakeri* is deemed a priority, I suggest that a study concerning the feasibility of constructing a mammal-excluding fence around the core *C. whitakeri* site be commissioned immediately.

In the face of synergistic effects between habitat change and complex arrays of interacting introduced species, the use of exclosures is an increasingly attractive option. As has been demonstrated elsewhere in New Zealand (e.g., Tocher 2006), the alternative is to commit to long term and extremely expensive studies that seek to identify agents of decline while the species at most risk continue to decline or disappear.

CHAPTER 3

Spatial avoidance enables the large, nocturnal gecko Hoplodactylus duvaucelii to persist with invasive kiore,

*Rattus exulans*⁴

3.1 Abstract

Rodents are efficient invaders on a global scale and pose a significant threat to native biotas, particularly in systems without native predatory mammals. Kiore, *Rattus exulans*, are implicated in extinctions, range restrictions and declines of endemic faunas throughout the Pacific. However, research into the behavioural and ecological modifications that enable native species to persist in presence of kiore is scant. I examined the population structure, behaviour and microhabitat use of Duvaucel's gecko, *Hoplodactylus duvaucelii* (radio-telemetry), and kiore (spool-and-line tracking) on three New Zealand offshore islands with different histories of rat invasions and eradication: (1) Green Island, historically rat-free, (2) Korapuki, eradicated of rats 20 ya, and (3) Ōhīnau, before and six months after rat eradication. Although kiore and Duvaucel's geckos shared habitat at a broad spatial scale, little overlap in micro-habitat use existed where they were sympatric. In the presence of rats, Duvaucel's gecko capture rates were low and recruitment was reduced. However, six months after rat eradication and prior to any recruitment, capture rates of adult geckos increased four-

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fold, and geckos were using a greater proportion of habitat preferred by rats, providing strong empirical evidence that kiore ecologically displace Duvaucel's geckos. Spatial avoidance behaviour by geckos is a highly plastic response to the presence of rats that may have enabled their persistence at a reduced density on kiore-inhabited islands.

3.2 Introduction

Biological invaders pose a primary threat to native ecosystems and biodiversity on a global scale (e.g., Soulé 1990, Vitousek *et al.* 1996, Long 2003). Island biotas usually comprise a reduced suite of sympatric species, as island size and resources limit species diversity. Such biotas are particularly vulnerable to invasive species (e.g., Case & Bolger 1991). The introduction of novel predators and competitors has therefore been instrumental in shaping biogeographic patterns on islands (Cassels 1984, Case & Bolger 1991). Rodents are efficient invaders and have been implicated in the extinction, range reduction and decline of endemic faunas (e.g., Amarasekare 1994, Steadman 1995, Stapp 2002, Towns *et al.* 2006). In a well documented example, the introduction of kiore (Pacific rats; *Rattus exulans*) to New Zealand is widely believed to have initiated large-scale biogeographic changes to native fauna, which were exacerbated by subsequent mammalian introductions (Cassels 1984, Worthy & Holdaway 2002, Towns *et al.* 2006).

Several historical and evolutionary processes have contributed to the enhanced susceptibility of the native New Zealand fauna to introduced mammals (Daugherty *et al.* 1993). New Zealand's biota evolved in the absence of terrestrial mammals (except for three species of bats; Daniel & Williams 1984) since its separation from Gondwana ca. 80 mya (King 2005). As a result, many species evolved to occupy ecological niches filled elsewhere by small mammals (e.g., Duthie *et al.* 2006), and may lack appropriate

antipredator responses to introduced mammals (Worthy & Holdaway 2002, Chapters 4 & 5, Appendix 1). The long lifespans and low reproductive rates characteristic of New Zealand endemic animals, especially reptiles (Daugherty *et al.* 1993, Cree 1994), are likely to exacerbate their vulnerability to invasive mammals.

Kiore, the first mammals introduced to New Zealand by humans (Matisoo-Smith *et al.* 1998), have been present on New Zealand's main islands at least since the time of Polynesian settlement approximately 1250-1300 AD (e.g., Anderson 1991, Brook 2000, Wilmshurst & Higham 2004), and possibly for 2000 years (Holdaway 1996). Subsequent to their initial invasion, kiore have been spread to many outlying islands at varying times (e.g., Brook 1999). Although kiore are now out-competed by other introduced rodents throughout much of New Zealand mainland (Yom-Tov *et al.* 1999, Atkinson & Towns 2001, Ruscoe 2004, Russell & Clout 2004), they continue to pose a major threat to native fauna on many northern offshore islands (Dingwall *et al.* 1978). Evidence from video surveillance, population manipulations and post-eradication monitoring strongly indicates that recruitment and abundance of a range of native taxa are negatively affected by kiore (reviewed by Towns *et al.* 2006).

Biogeographic changes in New Zealand's native biota resulting from predation and competition by invasive mammals are well documented (e.g., Towns & Daugherty 1994), yet the mechanisms enabling some species to coexist with invasive mammals have received little research attention (Towns *et al.* 2006). At a global scale, both native and introduced predators induce behavioural, ecological, habitat, and morphological shifts in their prey (e.g., Schoener 1975, Pacala & Roughgarden 1985, Losos *et al.* 2004, Sax *et al.* 2005). Understanding how these predator-induced shifts enable native species to persist in the presence of introduced predators is vital in order to formulate conservation strategies for threatened species. New Zealand is an ideal location to conduct field 'experiments' investigating the behavioural and ecological responses of native species to invasive mammals because: (1) introduced mammals have shaped distribution patterns of many species (Worthy 1987, Towns & Daugherty 1994), (2) mammalian invasions of New Zealand's 297 offshore islands of >5 ha have been patchy (Atkinson & Taylor 1991, Russell & Clout 2005), and (3) currently favoured conservation strategies involve mammalian eradication from islands (Atkinson & Towns 2001, Dilks & Towns 2002, Towns & Broome 2003, Appendix 2) and subsequent restoration. Hence, islands of close geographic proximity with varying histories of mammalian invasions and eradication provide a powerful natural experimental framework in which to explore the impacts of introduced mammals on native biota (Simberloff 2001).

Many of New Zealand's endemic reptiles are severely affected by introduced mammals due to predation and competition (Towns & Daugherty 1994). For example, invasive rats are believed to be responsible for the fragmented distribution of the large, nocturnal skinks *Cyclodina alani, C. macgregori* and *C. whitakeri* (Whitaker 1978, Towns & Daugherty 1994). Duvaucel's gecko, *Hoplodactylus duvaucelii*, is New Zealand's largest extant gecko (Gill and Whitaker 1996). Subfossil evidence indicates that its present disjunct distribution is a relic of its range prior to mammalian invasions (Worthy 1987); it now exists only on offshore islands to the north-east of New Zealand and in Cook Strait (Gill & Whitaker 1996). However, kiore are present as the only introduced predatory mammal on >50% of northern islands inhabited by Duvaucel's geckos (Towns 1991). Observations on these islands indicate that lizards: (1) are up to 25 times more abundant on the shore and in coastal cliffs and boulders than in forested areas in the presence of kiore (Whitaker 1978), (2) may occur in a reduced range of habitat types in the presence of introduced rats (Towns 1996), and (3) may show modified demographic structure in the presence of rats (Towns 1991), though much of

this has never been tested. A recent review (Towns *et al.* 2006) calls for deficiencies in knowledge of the impacts of introduced rats to be remedied through comprehensive measurements of the responses of indigenous species to rat eradications.

Here I provide the first empirical test of whether introduced kiore induce modified population structure, behaviour and habitat use in a native species, Duvaucel's gecko, with which it shares similar temporal (nocturnal activity phase) and ecological (body size, diet, habitat use) niches (Bettesworth 1972, Newman & McFadden 1990, Ussher 1995, Atkinson & Towns 2005). I investigated habitat use by: (1) Duvaucel's geckos on three islands with different histories of kiore introduction and eradication, and (2) kiore sympatric with geckos, to assess how Duvaucel's geckos are able to persist in the presence of kiore when other relatively large endemic reptiles commonly experience local extinction. I specifically test three hypotheses:

- Kiore influence population structure of Duvaucel's geckos by limiting recruitment;
- 2. Sympatric Duvaucel's geckos and kiore use micro-habitat differently;
- 3. Duvaucel's geckos show a behavioural response to removal of kiore by using a greater proportion of rat-preferred habitat after rat eradication.

3.3 Methods

3.3.1 Study species

Duvaucel's geckos are large (snout-vent length (SVL) up to 160 mm, mass up to 118 g; Whitaker 1968), nocturnal, terrestrial and arboreal geckos, with a long lifespan (at least 36 years in the wild; Thompson *et al.* 1992). Sexual maturity is reached at seven years of age, and females give birth to 1-2 young annually in February-May,

following a 7-8 month gestation period (Barwick 1982, Cree 1994, Gill & Whitaker 1996).

Kiore are also nocturnal, and are agile climbers, feeding and occasionally nesting in trees (Atkinson & Towns 2005). They generally weigh 60-80 g, though maximum recorded mass is 180 g, and head-body length (HBL) is up to 180 mm (Atkinson & Towns 2005). Reproduction varies greatly among sites. However, as an indication, females on a nearby island (Tiritri Matangi) produced 19-21 young per year (in three litters; Moller & Craig 1987). Diets of kiore and Duvaucel's geckos overlap; both consume primarily invertebrates, though plant material, occasional reptiles and (in the case of kiore) birds are included in the diet (Barwick 1982, Christmas 1995, Atkinson & Towns 2005).

3.3.2 Study sites

My study was conducted on three offshore islands (Fig. 1): (1) Ōhīnau (44 ha), where kiore were eradicated in 2005 (R. Chappell, pers. comm.); (2) Green Island (3 ha), always mammal-free; and (3) Korapuki (18 ha), kiore eradicated in 1986 (Towns 1991). European rabbits, *Oryctolagus cuniculus*, were also present on Korapuki and Ōhīnau, but eradicated in 1987 and 2005, respectively. Rabbits are herbivorous and therefore unlikely to affect Duvaucel's geckos through predation or resource competition. However, rabbits modify vegetation composition and structure which may indirectly influence geckos. The geographic proximity of these islands (maximum distance between islands is 8.8 km and all are 4.5-7.3 km distant from the mainland North Island; Fig. 1) limited climatic and latitudinal variability between sites. All research was conducted in February and March, to minimise the influence of season on behaviour. Week-long research trips were made to: (1) Ōhīnau in February/March 2005



Figure 1. A map of the Mercury and Ōhīnau Island groups, east of the Coromandel Peninsula, North Island, with New Zealand inset. Islands on which Duvaucel's geckos, *Hoplodactylus duvaucelii* (pictured) were radio-tracked are labelled. Kiore, *Rattus exulans*, inhabited Korapuki until 1986 and Ōhīnau until 2005. Green Island has always remained free of introduced mammals.

six months prior to rat eradication, and February 2006 six months after rat eradication, (2) Green Island in February/March 2006, and (3) Korapuki in March 2006.

All three islands are dominated by coastal forest comprising extensive areas of mahoe, *Melictyus ramiflorus*, and a coastal fringe of pohutukawa, *Metrosideros excelsa*, above rocky beaches. Search areas on all islands included forest habitat and a coastal transect on boulder beaches above the high tide line. On Ōhīnau, the mahoe forest on the north-west face of the island and a 230 m coastal transect were searched for Duvaucel's geckos and trapped for kiore. The gecko search area on Green Island comprised of a 470 m transect along the coastal boulders and forest margin on the southern half of the island. On Korapuki, an 84 m transect through coastal boulders and

a 176 m forest transect on the south-west side of the island were searched. Available habitat was measured on all islands by recording microhabitat variables (substrate type, presence/absence and type of cover 0.3 m above ground, canopy species and canopy height) at 5 m intervals along randomly chosen transect lines perpendicular to search transects.

Ambient temperature was recorded hourly at each study island using waterproof Stowaway[®] TidbiT[®] temperature loggers (Onset Computer Corporation, Massachusetts). Loggers were placed 2 m above ground beneath closed canopy for the duration of each research trip.

3.3.3 Capture and radio-tracking of Duvaucel's geckos

Duvaucel's geckos were located primarily through night-searching, but were also captured opportunistically at night and during the day (in diurnal retreat sites) whilst radio-tracking. For each gecko captured, I recorded morphometric information including SVL (to 1 mm) and mass (on a Pesola spring balance to 1 g; Table 1). Up to 10 adult geckos were fitted with radio transmitters and tracked at any one time, though total number tracked per island may be >10 as individuals that lost transmitters (battery failure or geckos escaping from harnesses) were replaced in the study.

Telemetry is an accepted method for tracking New Zealand geckos (Christmas 1995, Schneyer 2001, Salmon 2002, Appendix 1). Transmitters (0.9 g total weight and <5 % of gecko body weight; Sirtrack, New Zealand) were attached to geckos using an external backpack following the methods of Salmon (2002). The main harness, made of a polyamide and cellulose contour bandage (15 x 60 mm; Easifix B) was strengthened with shoulder straps made of hypoallergenic self-adhesive fabric strips (7.5 cm x 3 mm; Mefix B). Fabric of backpacks was dyed black, according to the colour of the gecko,

 Table 1. Morphometric data for adult kiore, *Rattus exulans*, and Duvaucel's geckos, *Hoplodactylus duvaucelii*, captured on Ōhīnau, Korapuki and

 Green Islands in February/March 2005 and 2006. * HBL = head-body length (rats only); SVL = snout-vent length (geckos only).

Island	Year	Rodent status	Species	Sex	Ν	HBL or SVL (mm)*			Mass (g)		
					-	mean (± SE)	min.	max.	mean (± SE)	min.	max.
Ōhīnau	2005	rats present	rats	female	17	146.5 (± 2.8)	122	161	91.5 (± 6.0)	50	145
				male	5	159.6 (± 5.3)	131	174	89.0 (± 5.3)	40	105
			geckos	female	4	118.3 (± 5.0)	105	127	43.1 (± 6.6)	28	60
				male	0	-	-	-	-	-	-
	2006	rats eradicated	geckos	female	13	122.0 (± 2.1)	107	133	54.1 (± 3.1)	34	70
		6 mo		male	9	127.0 (± 1.3)	121	133	61 (± 2.2)	48	70
Korapuki	2006	rats eradicated	geckos	female	31	122.4 (± 1.0)	108	134	53.4 (± 1.4)	38	68
		20 у		male	28	123.3 (± 0.7)	114	131	55.3 (± 1.3)	41	74
Green	2006	rat-free	geckos	female	15	122.8 (± 1.2)	113	133	54.5 (± 2.2)	37	67
				male	16	126.8 (± 1.2)	112	132	59.9 (± 1.9)	51	70
Green	2006	rat-free	geckos	female male	15 16	122.8 (± 1.2) 126.8 (± 1.2)	113 112	133 132	54.5 (± 2.2) 59.9 (± 1.9)	37 51	67 70

with a xylene-free permanent marker pen (Artline), to minimise the risk of transmitters attracting the attention of predators.

Each gecko was located hourly from 2100 h-0600 h NZDT each night using telemetry, and its position was marked to enable measurement of microhabitat variables the following day. The diurnal retreat site of each gecko was also located using telemetry.

3.3.4 Capture and spool-and-line tracking of kiore

Kiore were captured over two nights on Ōhīnau using Tomahawk[®] live traps (model #201) baited with a mixture of rolled oats and peanut butter. Twenty five traps, spaced at ca. 25 m intervals, were set in three parallel transect lines running perpendicular to the slope of the north-west face of Ōhīnau, along the coast and in forest at 15 m and 40 m asl. Twenty four kiore were captured over the 50 trap-nights. Morphometric information recorded for rats included head-body length (to 1 mm) and mass (on a Pesola spring balance to 1 g; Table 1).

Spool-and-line tracking provides micro-habitat information for rats at a resolution not possible using radio-tracking methodology (Jones & Barmuta 2000). Of the 24 kiore captured, 22 were measured, fitted with cotton spools (following methodology of Jones & Barmuta 2000) and subsequently tracked, one rat escaped, and the other was a recapture from the first trap night. I anaesthetised rats with isoflurane, trimmed the slick guard hairs, and attached spools (quilting cocoon bobbins of two-ply nylon thread from Coates Australia Pty Ltd, Sydney, encased in heat-shrink tubing) using cyanoacrylate ('superglue'). Spools were held in position for 1 min, the free end of the thread tied to a fixed point, and animals then released at the point of capture. Spools unravel from the inside of the bobbin, so that animal movement through the vegetation is not impeded by tracking. The first 10 m of line were excluded from habitat analyses, as this was considered to represent a flight response, after which microhabitat components were scored at 5 m intervals until the tracking line terminated. Length (and hence mass) of the spool attached to each individual was limited according to that individual's mass (137.2 m and 2.17 g for animals ≤ 80 g; 246.9 m and 4.27 g for animals >80 g). Habitat data and spools were collected within five days of attachment. Observation of spool-and-line devices revealed no interference with the cotton, but the remains of the package were chewed off, usually in 1-2 days.

3.3.5 Data collection and analyses

Sampling points were located every 5 m along a spool for rats and at each hourly telemetry position during the active phase for geckos. At each sampling point I measured substrate type (rock, leaf litter, flax litter, *Phormium cookianum*, tree root/trunk, boulders), canopy species and height, presence/absence and type of cover in the 0.3 m directly above the sampling point, horizontal movement and direction from the previous sampling point, and height of the animal above or below the ground. Data were then categorised into habitat types (based primarily on canopy species, but with reference to canopy height and substrate type), visibility, horizontal movements, and arboreal or subterranean movements, representing coarse- and fine-scale components of habitat use (Table 2). Animals were only included in statistical analyses of habitat use if data from a minimum of nine sampling points were collected, after excluding point of capture and diurnal retreat sites.

I investigated whether the presence of kiore drives the modification of population structure by comparing SVL frequencies of all Duvaucel's geckos captured on the three islands of differing rodent status. Gecko population structures for each island were generated from 2006 capture data only, as individuals were not permanently marked on **Table 2.** Habitat use characteristics of Duvaucel's geckos (G), *Hoplodactylus duvaucelii*, and kiore (R), *Rattus exulans* on islands in the Mercury and Ohīnau groups, north-eastern New Zealand.

Type of data	Species	Categories	Definitions and methods
Habitat type	G,R	a	Coastal cliffs or boulders
		b	Poroporo, Solanum aviculare (in fruit)
		c	Dense area of coastal flax, Phormium cookianum
		d	Forest dominated by pohutukawa, Metrosideros excelsa; karo, Pittosporum crassifolium
		e	Other coastal forest (taupata, Coprosma repens; karamu, C. robusta; karaka, Corynocarpus
			laevigatus, kawakawa, Macropiper excelsum; Melicytus novae-zelandiae; mahoe, M. ramiflorus;
			ngaio, Myoporum laetum; woolly nightshade, Solanum mauritianum)
		f	Open forest (no canopy)
Visibility	G,R	NV	Not visible, i.e. covered in 0.3 m directly above animal
		V	Visible, i.e. no cover in 0.3 m directly above animal
Arboreal use of	G,R	А	Arboreal; animal ≥ 0.1 m above ground
habitat		G	Ground
		S	Subterranean; animal ≥ 0.1 m below ground

Ōhīnau in 2005 and may have been recaptured during the 2006 trip. Capture rates presented are based on active searching (not opportunistic captures of geckos whilst radio-tracking), and though influenced by vegetation structure, height and density, provide an indication of gecko abundance. Samples sizes for comparisons of capture rates based on search effort (Table 3) and morphometrics (Table 1) exceed those of the habitat use analyses (Table 4), as they were recorded for all animals captured.

Data were analysed in the statistical programme 'R' (version 1.9.1; R Development Core Team, 2004). Statistical significance is assumed at $\alpha = 0.05$. All data satisfied the assumptions of the statistical tests used and are presented as mean ± SE, unless stated otherwise. In order to statistically compare habitat use by geckos and rats, I assumed that the spatial generation of sampling points for rats was representative of temporal habitat use.

For all habitat use analyses, the length of time an individual spent in one habitat type (termed the 'interval') without movement (and hence inability to switch between habitats) was used as the unit of replication. Gecko movements of <0.5 m in an hour were deemed insufficient to move into a different habitat type and counted as a lack of movement. Habitat availability was defined as the proportion of sampling area within an island covered by a habitat type.

Bray-Curtis analyses are commonly used in ecology to measure dissimilarity between groups based on continuous variables (Quinn & Keough 2002). I used Bray-Curtis Dissimilarity (BCD) to measure the magnitude of discrepancies between expected habitat use (based on availability, or habitat use by another focal group of geckos or rats) and observed use. To test the significance of the BCD value, I generated a null distribution of the observed dissimilarity (pseudo-BCD) by assuming no population dissimilarity and resampling the intervals using the assumed habitat **Table 3.** Search effort and captures of Duvaucel's gecko, *Hoplodactylus duvaucelii*, on Ōhīnau, Korapuki and Green Islands, New Zealand, in February/March 2005 and 2006. 'CPUE' stands for catch per unit effort, and was calculated from dedicated search effort, whereas 'total geckos caught' included opportunistic captures while radio tracking other individuals. Ambient temperature (temp.) was recorded hourly between 2100 and 0700 h NZDT at 2 m above ground under a closed canopy. * A maximum of 10 geckos were tracked at any one time.

Island	Year	Nights	Mean temp. (°C) ± SE	Rodent status	Total geckos caught	Geckos radio- tracked*	Hours searched	Geckos captured through direct searching	CPUE
Ōhīnau	2005 2006	6 7	19.5 (± 0.2) 19.6 (± 0.1)	rats present rats eradicated 6mo	4 25	4 19	7 10.6	2 13	0.29/hr 1.23/hr
Korapuki	2006	7	18.5 (± 0.1)	rats eradicated 20y	90	20	5.6	26	4.64/hr
Green	2006	7	18.0 (± 0.2)	rat-free	37	14	8.3	16	1.93/hr

Species	Kiore		Duvaucel's geckos							
Rodent status			Rats pr	resent	Rats absent					
Island & year	Ōhīnau 2005 10 (256)		Ōhīnau 2005 3 (45)		Ōhīnau 2006 10 (211)		Korapuki 2006 8 (138)		Green Is. 2006 11 (228)	
N individuals (observations)										
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Percentage of total locations in										
a. Coastal cliffs/boulders	7.3	6.3	44.6	25.7	13.8	4.7	0	-	11.4	7.2
b. Poroporo	10.2	3.6	0	-	0	-				
c. Coastal flax	5.5	3.9	0	-	6.5	4.3	30.7	12.6		
d. Pohutukawa/karo forest	10.8	6.4	0	-	2.6	1.7	50.9	16.2	35.0	10.4
e. Other coastal forest	62.1	10.9	53.3	23.9	74.0	6.6	18.4	7.9	47.1	12.0
f. Open forest	4.1	1.6	2.1	2.1	3.2	1.2	0	-	6.5	6.2
Percentage of observations without cover	77.4	4.5	8.3	8.3	28.7	8.2	16.6	8.5	11.1	3.2
Percentage of time spent										
Above ground	14.0	3.8	50.4	26.2	47.8	8.7	52.9	13.2	40.9	9.3
On the ground	85.0	3.9	34.6	27.5	43.1	6.4	46.7	13.0	38.3	7.6
Subterranean	1.0	0.5	15.0	15.0	9.1	3.9	0.4	0.4	20.8	8.9

Table 4. Summary statistics of habitat-use parameters for Duvaucel's geckos, *Hoplodactylus duvaucelii*, that are sympatric (Ōhīnau, 2005) and allopatric (Ōhīnau, Korapuki and Green Island, 2006) with kiore, *Rattus exulans*. Grey shading indicates that a habitat type is unavailable.

proportions through Monte Carlo testing. Using this statistical methodology I tested significance of the following habitat use patterns:

- Habitat use relative to availability by each population of Duvaucel's geckos and by kiore, within an island;
- Habitat use by Duvaucel's geckos in the presence of kiore (Ōhīnau, 2005) relative to: (1) habitat use by kiore, and (2) Duvaucel's gecko habitat use on the same island, six months after the eradication of kiore;
- Habitat use by Duvaucel's geckos on islands with differing histories of interaction with kiore, accounting for variation in habitat availability.

Standardised interval lengths were taken where groups were compared in order to swap intervals between groups to generate a pseudo-BCD. In the case of habitat availability differing between islands, the lengths of intervals were re-scaled. For analyses involving different islands, data were excluded if a habitat type was unavailable on any island and Manly's α was used as a test statistic to measure habitat selection allowing for different habitat availability. A Bonferroni adjustment was made when each habitat type was analysed separately to account for multiple testing.

3.4 Results

The presence of kiore appears to restrict recruitment into Duvaucel's gecko populations. While Duvaucel's gecko populations on rat-free Green Island and Korapuki showed a normal size distribution pattern, the population on $\bar{O}h\bar{n}au$ (which was sympatric with rats until 2005) was skewed towards larger individuals (Fig. 2). The smallest gecko caught on $\bar{O}h\bar{n}au$ was a female with SVL of 97 mm and only 4 % of geckos caught were in the 50 – 100 mm SVL size class. Smaller geckos were caught on Korapuki and Green Island: the smallest geckos had SVLs of 54 mm and 65 mm,



Figure 2. Population structure of Duvaucel's geckos, *Hoplodactylus duvaucelii*, based on gecko captures on islands with varying histories of interaction with kiore, *Rattus exulans* in February/March 2006. Green Island (white bars) has never had rats, and rats were eradicated from Korapuki (grey bars) in 1986 and Ōhīnau (black bars) in 2005. No recruitment occurred in the Ōhīnau population between rat eradication and gecko sampling.

and the 50 – 100 mm SVL size class contained 24 % and 14 % of individuals, respectively. However, maximum SVL of adult geckos was similar on all three islands (within 1 mm; Table 1). Inter-island variability in adult gecko body size and mass was minimal (Table 1), but adult males were significantly larger and heavier than adult females (SVL 125.0 \pm 0.6 mm vs. 122.4 \pm 0.8 mm, and 57.6 \pm 1.0 g vs. 53.8 \pm 1.1 g, respectively). On Ōhīnau, adult kiore were both larger and heavier than Duvaucel's geckos, though adult body size overlapped between the two species (Table 1).

The capture rate of Duvaucel's geckos was substantially reduced in the presence of kiore (Table 3). On Ōhīnau in 2006 capture rate was 1.23 geckos per person hour, a four-fold increase from the 0.29 geckos per person hour achieved in February/March 2005, when kiore were still present on the island (Table 3). Capture rates of geckos were higher on rat-free Green Island and Korapuki (1.93 and 4.64 geckos per person hour, respectively; Table 3) than those on $\bar{O}h\bar{n}au$, despite night-time temperatures being consistently 1.0 - 1.5 °C higher on $\bar{O}h\bar{n}au$ (Table 3).

Thirty two Duvaucel's geckos and ten kiore followed during the study were included in statistical analyses of habitat use (Table 4). Most geckos and rats used a variety of structurally disparate habitat types. Eighty one percent of geckos switched between habitat types (defined in Table 2), of which 69% moved between coastal and forest habitats. All kiore switched between habitat types; half moved only within the forest habitat, and the other half used both forest and coastal habitats.

Duvaucel's geckos on northern New Zealand islands used a range of habitat types from the shore, through coastal flax and pohutukawa, to the forested interior (Fig. 3). However, use of some habitat types relative to availability differed among gecko populations from islands according to rodent status. On rat-free Green Island and Korapuki (Fig. 3c & 3d, respectively) use of coastal cliff and boulder habitat was low relative to availability (p < 0.0001 for both), while on Õhīnau in 2005 (while kiore were present; Fig. 3a) it was relatively high (BCD = 0.3778, p = 0.0042), and in 2006 (six months after rat eradication; Fig. 3b) it was in proportion to availability (BCD = 0.1188, p = 0.8752). In contrast, use of coastal flax habitat was high relative to availability on rat-free Korapuki (Fig. 3d; BCD = 0.3066, p = 0.0012), but not used by geckos on Õhīnau when rats were present (Fig. 3a) and used less than expected on Õhīnau six months after rat eradication (Fig. 3b; BCD = 0.0396, p < 0.0001).

Sympatric Duvaucel's geckos and kiore differed in habitat use (BCD = 0.6581, *p* < 0.0001; Fig. 4). Though coexisting in a range of habitats at a broad scale, from the boulder beach through the mahoe forest, geckos and rats used distinct micro-habitats and niches within these habitats (Table 4; Fig. 4). Rats were found predominantly at ground level (85.0 ± 3.9 % of all samples; Table 4), but ventured up to the top of fruiting poroporo trees (~3.5 m above ground) to feed. Rats spent 36.5 % of time in a

foraging pattern (defined as thread pattern from previous 5 m weaving so that distance between sampling points < 3 m) in poroporo, even though it represented only 10.2 % of habitat used. In contrast, geckos used a greater vertical component of habitat, particularly within the mahoe-dominated forest and coastal cliffs and spent more time under cover than rats (Table 4). I observed no overlap between gecko and rat use of the following habitats: fruiting poroporo trees, coastal flax, pohutukawa trees (all rats only) and coastal cliff crevices (geckos only; Fig. 4). Kiore were seldom observed in karaka



Figure 3. Observed habitat use by Duvaucel's geckos, *Hoplodactylus duvaucelii*, versus that expected based on availability in six habitat types on offshore islands in the Mercury and Ōhīnau groups, New Zealand. Localities are Ōhīnau (sampled in (a) 2005, six months prior to eradication of introduced kiore, *Rattus exulans*, and in (b) 2006, six months after kiore eradication), (c) Green Island (always rat-free), and (d) Korapuki (eradicated of kiore 20 ya). Dotted lines represent observed habitat use by geckos and solid lines represent habitat availability for each habitat type within an island. Striped shading of bars indicates overlap between observed habitat use and that expected based on availability; open bars indicate the difference between observed and expected habitat use. Habitat types are: a) coastal cliffs and boulders, b) poroporo, *Solanum aviculare* (in fruit), c) coastal flax, d) pohutukawa, *Metrosideros excelsa*, or karo, *Pittosporum crassifolium*, forest, e) other coastal forest, and f) open forest.



Figure 4. Habitat selection of Duvaucel's geckos, *Hoplodactylus duvaucelii*, and kiore, *Rattus exulans*, in sympatry on Ōhīnau, a New Zealand offshore island, in February/March 2005 and by Duvaucel's geckos six months after rat eradication, in February 2006. Habitat types are: a) coastal cliffs and boulders, b) poroporo, *Solanum aviculare* (in fruit), c) coastal flax, d) pohutukawa, *Metrosideros excelsa*, or karo, *Pittosporum crassifolium*, forest, e) other coastal forest, and f) open forest.

trees, *Corynocarpus laevigatus*, which had just finished fruiting at the time of the study, and in which geckos spent a disproportionate amount of time.

Duvaucel's geckos occupied available habitat differently six months after kiore eradication, compared with when they were sympatric with rats (BCD = 0.3793, p = 0.0411; Table 5). In February/March 2005, while kiore were present on Ōhīnau, radiotracked Duvaucel's geckos did not use fruiting poroporo forest, coastal flax or pohutukawa forest and none were located in these habitat types during night searches. By February 2006 (six months after rat eradication) geckos were using the latter two habitat types (Fig. 4). More geckos were caught in the mahoe-dominated coastal forest **Table 5.** Results of Bray-Curtis Dissimilarity (BCD) analyses of habitat-use by Duvaucel's geckos, *Hoplodactylus duvaucelii*, that are sympatric(Ōhīnau, 2005) and allopatric (Ōhīnau, Korapuki and Green Island, 2006) with kiore, *Rattus exulans*.

	Duvaucel's geckos									
Rat status	Rats	present	Rats absent							
Island and year	Ōhīn	au 2005	Ōhīn	au 2006	Korapuki 2006		Green Is. 2006			
N intervals			103	51		98				
	BCD	Р	BCD	Р	BCD	Р	BCD	Р		
Duvaucel's geckos Ōhīnau 2006	0.3793	0.0411*	-	-	-	-	-	-		
Korapuki 2006	0.9517	<0.0001*	0.8848	<0.0001*	-	-	-	-		
Green Island 2006	0.6446	<0.0001*	0.6481	<0.0001*	0.1010	0.5431	-	-		

after rat eradication, and thus in coastal forest relative to coastal boulders and cliffs (Fig. 4). I also observed a change in selection of diurnal retreat sites by geckos after rats were eradicated from $\bar{O}h\bar{n}au$. Following eradication, geckos used retreats that were 0.8 m lower, and a greater proportion were located in forest habitat (71% compared with 57% in 2005) relative to coastal boulders and cliffs. Habitat use by rats on $\bar{O}h\bar{n}au$ in 2005, prior to their eradication, was less similar to geckos while they were sympatric (February/March 2005; d = 0.6581) than to geckos six months after rat eradication (February 2006; d = 0.5086), though not significantly so (p = 0.0658).

Habitat use by Duvaucel's geckos did not differ between control islands (i.e., Korapuki, eradicated of rats 20 ya, and Green Island, always rat free; BCD = 0.1010, p = 0.5431; Table 5). However, habitat use by geckos on rat-inhabited Ōhīnau differed from both control islands before and six months after kiore eradication (p < 0.0001 in all cases; Table 5).

3.5 Discussion

Deficiencies in knowledge of the mechanisms of introduced rats on native fauna limits our ability to effectively manage and restore vulnerable populations and ecosystems. Towns *et al.* (2006) call for comprehensive measurements of the responses of indigenous species to rat eradications. I provide detailed habitat use from a largescale, 'natural' experiment to demonstrate that Duvaucel's geckos modify behaviour in response to the presence of kiore, which is likely to reduce predatory encounters. Capture rates of Duvaucel's geckos were reduced in the presence of kiore, as evidenced by a four-fold increase in adult gecko captures six months after rat eradication. Greater visibility of Duvaucel's geckos following rat removal implies that geckos spatially avoid rats through either being less conspicuous, or using habitats not preferred by rats. As geckos used more rat-preferred habitat following rat eradication, I provide empirical support for the latter mechanism, though do not rule out the former. Spatial avoidance behaviour appears to allow these large, nocturnal geckos to survive in sympatry with rats at a reduced density, at least in the short term.

3.5.1 Influence of introduced rodents on recruitment patterns

Kiore appear to limit recruitment into Duvaucel's gecko populations. On ratinhabited Ōhīnau, the Duvaucel's gecko population is skewed towards larger individuals, relative to Korapuki and Green Island where a full spectrum of size classes are found (Fig. 2). Juveniles may have comprised a greater proportion of the population than was reflected by search effort on \overline{Oh} īnau. However, I consider this unlikely as, (1) juveniles were found using the same search technique on Green Island and Korapuki, and (2) kiore prey on lizards (Bettesworth 1972, McCallum 1986) and juvenile tuatara (Newman 1988) similar in size to juvenile Duvaucel's geckos. I therefore interpret the absence of juvenile geckos in the Ōhīnau population as a real skew in population structure towards larger individuals, which are more likely to survive predation attempts by kiore. However, persistence of Duvaucel's gecko populations on islands with kiore suggests that either (1) recruitment is reduced to low levels but is sufficient for populations to survive at reduced densities, or (2) we are witnessing a snapshot of the extinction process driven by recruitment failure induced by predatory rats. As the timing of kiore arrival on offshore islands is highly variable (Brook 1999), and not known for Ōhīnau, these alternative hypotheses cannot be resolved with the present data. However, as Duvaucel's geckos are inexplicably absent from at least two islands previously inhabited by kiore (Cuvier and Red Mercury), extinction cannot be discounted (D. Towns pers. comm.).

Duvaucel's geckos are the largest extant New Zealand geckos (65 mm SVL larger than any other native species; Gill & Whitaker 1996), and have young similar in size to the adult size of many other gecko species in northern New Zealand. That this size class appears most vulnerable to predation by kiore parallels the severe population level impacts or local extinctions of smaller geckos (e.g., *H. pacificus*; *H. maculatus*) on islands invaded by kiore (e.g., Towns 2002b). Meanwhile, rats induce recruitment failure among the larger endemic reptiles, (e.g., tuatara, *Sphenodon punctatus*; Cree *et al.* 1995), thus posing a threat to long-term population persistence.

3.5.2 Behavioural responses to introduced predators

Capture rates of Duvaucel's geckos are lower on rat-inhabited islands than on ratfree islands (Christmas 1995; Table 3). Evidence of suppressed gecko recruitment on rat-inhabited Ōhīnau suggests that gecko densities are limited by the presence of rats. However, the four-fold increase in adult Duvaucel's gecko capture frequency just six months after rat eradication, indicates that geckos are also less visible in the presence of rats and that relatively low capture rates on rat-inhabited islands are partially attributable to gecko behavioural shifts. My findings extend an observation of increased visibility of Mauritian skinks, *Scelotes bojerii* and *Cryptoblepharus boutonii* immediately after eradication of Norway rats, *R. norvegicus* from Gunner's Quoin (Bell 2002).

The behavioural response to spatially avoid introduced rats demonstrated for Duvaucel's geckos may be applicable to rat-affected lizard populations more generally. In 2006, six months after the eradication of kiore from Ōhīnau, I found an individual from each of a smaller, congeneric gecko species (*H. maculatus*; to 82 mm SVL; Gill & Whitaker 1996) and a small, diurnal/crepuscular skink species (*Cyclodina aenea*, to 62 mm SVL; Gill & Whitaker 1996; J. Hoare, unpubl. data). Until then, neither of these species had been found on Ōhīnau since 1972 (A. Whitaker, unpubl. data) and were feared to be locally extinct (R. Chappell, pers. comm.). In a similar case, night geckos, *Nactus coindemirensis*, were rediscovered on Gunner's Quoin, Mauritius, following eradication of Norway rats, after being previously known from only two specimens (Bell 2002). Behavioural responses of a variety of gecko and skink species to rat eradication demonstrate the need to allow for a temporal lag (also see Towns 2002a) between eradication and any restorative translocations.

Although many New Zealand species have proven extremely vulnerable to predation by invasive mammals, many taxa that coexist with mammals have done so via behavioural modification (Bremner *et al.* 1989, McIntosh & Townsend 1994, Rufaut 1995, Rufaut & Gibbs 2003). Bremner *et al.* (1989) report more pronounced escape responses of a variety of arthropods on islands with mammalian predators compared with those that are mammal-free. A post-eradication survey of tree weta, *Hemideina crassidens*, indicated that native orthopterans respond to kiore eradication by increasing activity and using habitat closer to the ground (Rufaut & Gibbs 2003). Additionally, common geckos, *Hoplodactylus maculatus* were more frequently encountered at ground level, and at higher rates, on a mammal-free New Zealand offshore island (Mana) than a neighbouring one (Kapiti) where Pacific and Norway rats were present (Gorman 1996). Similar patterns are observed for Duvaucel's geckos; the four-fold increase in capture rate following eradication indicate ecological release from rats, either through relaxation of cryptic behaviour or shifting into previously rat-preferred habitat.

3.5.3 Habitat use shifts driven by introduced predators

Ecological niches of Duvaucel's geckos and kiore overlap at a medium scale; both species use boulder beaches, coastal flax and the mahoe, pohutukawa and karo, *Pittosporum crassifolium*, dominated forests of New Zealand's northern offshore

islands (Towns 1991; this study). However, the few Duvaucel's geckos that were located in sympatry with kiore on Ohīnau showed little overlap with rats in microhabitat use (Fig. 4). Changes observed in micro-habitat use by Duvaucel's geckos following rat eradication during both active and inactive phases are consistent with release from predation risk posed by a ground-dwelling predator. I hypothesise that geckos had been marginalised in forest habitat due to the lack of available refugia from predatory kiore, but were able to re-establish in this habitat following rat removal (also see Towns 1991). Just six months after eradication of kiore from Ōhīnau, geckos were using a broader range of habitats compared with prior to eradication, all of which had been occupied by rats (Fig. 4). Similarly, crevices in coastal cliffs well above ground, were more frequently used as diurnal retreat sites prior to rat eradication. Such retreats are likely to provide better refugia from primarily ground-dwelling rodents than forest sites, but may be necessary to avoid native avian predators. My hypothesis is supported by pitfall-trapping data from Lady Alice Island where, two months after eradication of kiore, adult Duvaucel's geckos suddenly appeared in pitfall traps, implying a change in vertical habitat use to more terrestrial habitats (R. Parrish and D. Towns, unpubl. data; cited in Atkinson & Towns 2005).

Shifting habitat use to spatially avoid introduced rats may be a key behavioural mechanism enabling survival of native reptiles that share their temporal activity patterns (Whitaker 1978). The large nocturnal skinks of northern New Zealand (*Cyclodina alani, C. oliveri* and *C. whitakeri*), which are similar in size to Duvaucel's geckos, coexist with kiore on $\leq 11\%$ of islands where they occur (Towns 1991, Towns & Daugherty 1994) and may be more prone to extinction because of their limited ability to climb and therefore shift vertical use of habitat (Whitaker 1978). I suggest that Duvaucel's geckos avoid kiore by restricting most activity to crevices in cliffs and at boulder beaches, and by using the tops of trees, as opposed to the prevailing view that

they occupy the same habitats at lower densities (Whitaker 1978). Large nocturnal skinks, in contrast, are unable to use these habitat refugia and are instead limited to use of the ground, primarily in the forest, which can be easily accessed by rats (Whitaker 1973, 1978).

3.5.3 Management implications

Eradications have been overwhelmingly successful in releasing threatened reptile populations from mammalian predation and competition and allowing rapid population recovery. For example, capture frequencies of shore skinks, *Oligosoma smithi*, increased up to 50-fold on Korapuki in five years following eradication of kiore (Towns 1996). However, my data documenting behavioural shifts in a Duvaucel's gecko population following rat eradication demonstrate the need for caution when attributing increased capture rates to recruitment in long-lived animal species. Behavioural responses of native species to avoid detection by introduced predators may contribute to the difficulties associated with detecting vulnerable native species in rat-inhabited locations. Rapid population recovery of native species following rat eradications (e.g., Towns 1996) is likely to be initially attributable to a behavioural response to release from competition and predation (this study), followed by a demographic response (e.g., Towns 2002b).

CHAPTER 4

Chemical discrimination of food, conspecifics and predators by apparently visually-oriented diurnal geckos,

Naultinus manukanus⁵

4.1 Abstract

Animal life history strategies are often tightly linked to sensory cues. Squamate reptiles possess well developed chemosensory systems, which evolved early in their history and remain highly conserved. However, chemosensory abilities are secondarily reduced in primarily visual agamids and chameleonids and may not be important for this group. Diurnal geckos from New Zealand are primarily ambush foragers and avoid predators using visual crypsis. Reliance on visual cues may be a product of strong avian predation pressure and isolation from mammals and snakes for the past 80 my. I use New Zealand's diurnal geckos to test the role of local adaptation vs. evolutionary conservatism in defining chemosensory systems. Specifically, I test whether Marlborough green geckos, *Naultinus manukanus*, use chemoreception to detect and respond behaviourally to (1) food, (2) conspecific geckos of the opposite sex, and (3) native reptilian predators (tuatara, *Sphenodon punctatus*). Chemosensory cues mediated gecko interactions with all three stimuli tested: (1) the scent of fruit induced greater exploratory behaviour, (2) male geckos responded to conspecific female scent by

⁵ **Based on** Hoare, J.M., S. Pledger and N.J. Nelson. Chemical discrimination of food, conspecifics and predators by visually-oriented diurnal geckos, *Naultinus manukanus*. *Herpetologica* (in review)

increasing lingual sampling and activity, and (3) tuatara faecal cues elicited characteristic antipredator freeze behaviour in geckos, but skin secretions did not. Neither the primarily visual life history strategies nor the reduced range of predators of New Zealand's diurnal geckos appear to have reduced their chemosensory abilities relative to other non-iguanid squamate reptiles. Instead, my findings support the hypothesis that chemosensory traits remain highly conserved.

4.2 Introduction

The question of how selective pressures influence the evolution of species' traits is central to contemporary biology. Many species display suites of morphological and behavioural characteristics influenced by the primary sensory mechanism that they use. Squamate reptiles have highly developed chemosensory systems, which mediate a range of intra- and inter-specific interactions (Burghardt 1970, Gabe & Saint Girons 1976, Halpern 1992, Schwenk 1995). The evolution of chemosensory systems is considered conservative, and largely reflects suprafamilial attributes as opposed to local adaptation (Schwenk 1993). However, agamids and chameleonids are ambush foragers that rely on visual cues (Schwenk 1993, Cooper et al. 2001). As a consequence, these families have secondarily reduced chemosensory abilities (Parsons 1959, 1970, Gabe & Saint Girons 1976). Secondary loss of chemosensory abilities in some squamate families prompts the question of which criteria are necessary to precipitate an evolutionary switch from chemosensory to visual strategies. I test the role of local adaptation vs. evolutionary conservatism in defining chemosensory abilities of gekkotans that display primarily visual antipredator and prey detection strategies, perhaps as a result of their evolutionary isolation from many ground-dwelling predators.
The highly developed nasal chemosensory systems of most squamate reptiles enable their discrimination of many chemicals (reviewed by Schwenk 1995). Chemoreception in reptiles is known to be mediated by both the olfactory and vomeronasal systems, although other nasal chemical senses may also be involved (Halpern 1992). Tongue flicking allows lingual sampling of both substrates and the air via the vomeronasal organ, which enables discrimination between chemical signals and mediates behavioural responses (termed 'vomerolfaction'; Halpern 1992, Cooper 1996). Reptiles frequently rely on chemical cues to detect and avoid predators (e.g., Dial *et al.* 1989, Downes & Shine 1998, Downes 2002). Olfaction and vomerolfaction also mediate other interactions, e.g., with conspecifics (e.g., Cooper & Steele 1997, Bull *et al.* 2000, Cooper & Pèrez-Mellado 2002) and locating prey and other food (Cooper & Habegger 2000, Cooper & Pèrez-Mellado 2001).

Reptiles often use chemoreception in combination with other sensory cues, such as vision (e.g., Head *et al.* 2005). Under certain local conditions, visual cues may be of greater importance to reptiles and involve a trade-off with chemosensory ability (e.g., in agamids and chameleonids; Schwenk 1993). Although gekkotans have highly developed chemosensory abilities (Dial *et al.* 1989, Schwenk 1993, Cooper 1995b, Downes & Shine 1999), some have evolved secondary diurnality which may be associated with a switch to using primarily visual strategies. For example, diurnal green geckos, *Naultinus* spp., from New Zealand display visual crypsis and secretive behaviour as antipredator strategies and appear to rely on an ambush foraging mode for mostly invertebrate prey (Whitaker & Gaze 1999; Appendix 1).

The reliance of New Zealand's diurnal geckos on visual cues to avoid predators may have resulted from evolution in isolation from major predatory groups. On a global scale, major lizard predators are birds, reptiles (especially snakes) and mammals. In contrast, New Zealand had no terrestrial mammalian predators for ca. 80 my prior to the introduction of Polynesian rats, *Rattus exulans*, by Polynesian voyagers ca. 2000-1000 ya (Anderson 1996, Holdaway 1996), and today these remain absent from many offshore islands. Furthermore, snakes never established in New Zealand and there are no confirmed reports of terrestrial snakes in the New Zealand fossil record. Birds are the primary native predators of New Zealand lizards, and larger reptiles such as tuatara, *Sphenodon* spp., also prey upon lizards (Walls 1981). Because birds usually hunt from a distance, visual crypsis may assume a greater role in predator avoidance than the use of chemosensory cues to detect and spatially avoid predators. Similarly, tuatara appear to use primarily visual cues to detect their prey (Walls 1981, Meyer-Rochow 1988, Meyer-Rochow & Teh 1991). In contrast, reptiles (especially snakes) and mammals are proximate predators where chemoreception may play a key role in predator detection and avoidance by prey (e.g., Downes & Shine 1998). The visual antipredator strategy used by New Zealand's diurnal geckos may reflect an avian dominated predation regime, in contrast to the range of predators that elicit a chemosensory response in reptiles on a global scale.

The apparent lack of selection pressure to detect and avoid predators using chemoreception in New Zealand lizards may be countered to some degree by chemosensory use for foraging and mediating intraspecific interactions. New Zealand lizards (Diplodactylidae and Scincidae) are known to consume fruits and nectar (Whitaker 1987, Lawrence 1997, Wotton 2002), indicating potential use of chemoreception to find food sources. However, records of frugivory by the diurnal gecko genus *Naultinus* are sparse (Whitaker 1987), which leaves both the importance of fruit as a food source, and the mechanism involved in finding it, unresolved. Chemosensory conspecific recognition, and predator detection and avoidance, have not been examined in New Zealand geckos, though many possess distinctive femoral pores (e.g., Hitchmough 1982, Gill & Whitaker 1996) which may indicate the use of chemical signals to mediate conspecific interactions.

Adaptation to a reduced suite of predators and associated use of a visual-oriented strategy by New Zealand's diurnal geckos provides an opportunity to test the role of local adaptation vs. evolutionary conservatism in squamate chemosensory systems. I address two questions: (1) are chemosensory capabilities reduced in lizards that use primarily visual antipredator and foraging strategies? and (2) are chemosensory-mediated antipredator responses lost when prey are isolated from mammalian and snake predation pressure over evolutionary time? I address these questions by investigating chemosensory-mediated responses of diurnal, Marlborough green geckos, *Naultinus manukanus* to fruit, conspecifics and predators.

4.3 Methods

4.3.1 Study animals

Marlborough green geckos are small (up to 81 mm snout-vent length; Appendix 1) green, diurnal geckos which are restricted to the Marlborough region of New Zealand and occur in forest and scrub habitat (Gill & Whitaker 1996). These arboreal geckos exhibit limited movement patterns and appear to rely primarily on visual crypsis and secretive behaviour to avoid predators (Whitaker & Gaze 1999; Appendix 1).

Eighteen adult geckos (snout vent length (SVL) 62 – 81 mm; mass 5.7 – 11.9 g) captured from Stephens Island (Takapourewa), Cook Strait, New Zealand were held at Victoria University of Wellington between March and October 2003 (Hare 2005). Because Stephens Island has no introduced mammals or snakes (Brown 2000), lizards experienced a natural predation regime including only bird and reptilian predation prior to being taken into captivity. All 18 adult geckos (nine of each sex, eight females pregnant) were tested for behavioural responses to scent stimuli (fruit, conspecifics and native predators) over a three-week period in October 2003 during the normal mating season (Gill & Whitaker 1996). Previous work has shown that reproductive condition of female *Hoplodactylus maculatus* did not influence behaviour in scent trials (Chapter 5). Additionally, ten predator-naïve juvenile geckos (SVL 43 – 49 mm; mass 1.8 – 2.6 g) born to captive-held mothers were tested for behavioural responses to their native tuatara predators.

Adult geckos were kept individually in transparent plastic containers (330 x 215 x 110 mm, L x W x H) with 1 x 1 mm wire mesh (165 x 120 mm) in the lid for ventilation. Food and water were provided *ad libitum*; all other husbandry details are outlined by Hare *et al.* (2004). Juveniles were held under the same conditions as adults, though were housed in their birth groups (usually two individuals; three individuals in one case when one juvenile had no siblings). Following completion of this study, all geckos were translocated to Whakaterepapanui Island (Marlborough Sounds, New Zealand), as part of an ecological restoration programme.

4.3.2 Experimental procedure

Experimental methodology is based on Downes and Shine (1998). I tested behavioural responses of geckos to chemical cues of fruit, conspecific geckos and native reptilian predators to gauge the extent to which chemoreception mediated interactions. As lizards use tongue-flicking to sample substrates and airborne volatile compounds (vomerolfaction), the rate of tongue-flicking provides an objective index of chemosensory investigation (Cooper 1998, Cooper & Pèrez-Mellado 2002). A range of other behaviours were also recorded to provide context for any changes observed in tongue flicking rate (Downes & Shine 1998). I also investigated maintenance behaviour (eye-licking), activity and exploratory behaviour (walking, running, climbing, moving limbs and nudging the wall of the arena) and 'freeze' behaviour in relation to scent stimuli.

The experimental arena was a clear plastic enclosure (280 x 250 x 210 mm, L x W x H) containing a plain cotton cloth of the same dimensions as the base of the enclosure and covered with the scent to be tested. For juvenile geckos, the basal area of the experimental arena was reduced (to 250 x 130 mm) using a divider of the same material as the enclosure walls.

The cotton scent cloth was washed using a standard procedure prior to each trial, to remove any scent residue from previous trials. Washing treatment consisted of soaking the cloth in the disinfectant NapisanTM (active ingredient Sodium Percarbonate) for 2 h, rinsing thoroughly, air-drying and steam ironing. Behavioural responses of geckos to a washing control after the cloth had been treated with relevant scents (pear, conspecific gecko, tuatara skin secretions) were compared with their responses to a negative control (washed cloth which had not been in contact with any of the scents tested) to assess effectiveness of the washing methodology.

Scent treatments and controls were:

- (1) Negative control: unscented cloth,
- (2) Positive control: cloth sprayed with commercial cologne ('Smiley' Second Edition No. 42; Liberty Cosmetics Ltd, England),
- (3) Pear: cloth sprayed with a 1:1 solution of natural pear juice and distilled water,
- (4) Conspecific: cloth placed in an enclosure with a conspecific adult gecko of the opposite sex for 4 to 7 d,
- (5) Native predator skin secretions: cloth placed in an enclosure with an adult tuatara, *Sphenodon punctatus*, for a period of 16 to 24 h,
- (6) Native predator faeces: cloth covered in a slurry of tuatara faeces and distilled water.

The test enclosure was wiped with ethanol and allowed to dry between trials to remove lizard and test scents.

To avoid handling immediately prior to the experiment, geckos were placed into a plastic jar ca. 2 min prior to the experiment. The top third of the inner surface of the plastic jar was coated with Fluon[®] (Tetrafluoroethylene co-polymer), a paint with low surface tension to which geckos cannot adhere (Losos et al. 2001). Geckos were gently tipped into the enclosure at the start of the experiment.

Observations of behaviour commenced ca. 10 s after transfer of the gecko to the experimental enclosure. I observed continuously behaviours of geckos for 12 min from behind a cardboard hide. The observational data-logging programme ODLogTM (Macropod Software) was used to directly record behaviour onto the computer.

Either the frequency (1 and 2) or the duration (3 to 8) of the following behavioural acts and locomotor patterns was recorded:

- Tongue flick: the tongue is extruded and either waves it in the air, or lowers it to touch the substrate,
- (2) Eye lick: the tongue is slowly extruded and passed over an eye,
- (3) Slow walk: the gecko proceeds by either very slow, stalking or continuous movements of the limbs,
- (4) Run: very fast movement,
- (5) Climb wall: the gecko proceeds by movement of the limbs on the vertical surfaces,
- (6) Stationary, moving head, limbs or tail: the gecko moves body parts but does not alter its position in the enclosure,
- (7) Nudge wall: the gecko repeatedly presses its snout against a vertical surface of the enclosure,
- (8) Stationary, freeze: the gecko remains motionless.

Relative to a negative control, I predicted that scent of fruit and geckos would elicit elevated tongue flicking rates and greater exploratory behaviour, including either climbing or slow, deliberate walking. In contrast, I predicted that tuatara scent would elicit greater freeze behaviour and decreased movements, as visual crypsis is the usual mechanism by which these geckos avoid predators.

All geckos were conditioned to the experiment by undergoing three practice tests with a negative control prior to scent trials to minimise the influence of the novel experimental procedure on observed behaviours (Hare *et al.* 2004). Conditioning trials of nine adults and eight juveniles were recorded in order to assess the influence of the novel environment on gecko behaviour. All 18 adult *N. manukanus* were tested for behavioural responses to the negative control and to conspecific scent. From these, ten individuals were randomly selected to perform all other scent tests, including washing controls. All ten juvenile geckos were tested for behavioural responses to tuatara faecal cues against a negative control. Geckos were tested a maximum of one time in any day and order of the scent tests was randomly allocated. All tests were conducted within an ambient temperature range $(18.0 - 20.3 \,^\circ\text{C})$ over which this species is active (Werner & Whitaker 1978) during the normal activity (0900 to 2000 h NZDT; Appendix 1).

4.3.3 Statistical analyses

Data were analysed in the statistical programme 'R' (version 1.9.1; R Development Core Team, 2004). The individual is the unit of analysis. Continuous data were converted to proportions of total time spent in each activity and square roots of count data were taken for analyses. Statistical significance is assumed at $\alpha = 0.05$. All data are presented as mean ± SE, unless stated otherwise. All data satisfied the assumptions of the statistical tests used. To assess the effectiveness of the washing methodology at eliminating scent from the test cloths, I used data from adult geckos only and included data from all wash controls in relation to a negative control. The role of conditioning in minimising variation associated with novel behaviour was tested using data from the three successive conditioning trials recorded for nine adults and eight juveniles. Chemosensory abilities to detect the scent stimuli were assessed from behavioural responses of adults to the relevant scents (i.e., fruit, conspecifics and predators) in relation to a negative and positive control (washing controls were not included). Additionally, any ontogenetic change in chemosensory-mediated antipredator response was investigated by comparing adult and juvenile *N. manukanus* responses to tuatara faecal cues relative to a negative control.

Multivariate analyses of variance (MANOVAs), using the F approximation to the Wilks test, enabled me to assess the overall importance of the scent stimuli (as an independent variable), in explaining variation in behavioural actions (the dependent variables). Temperature, time of trial (early: 0900 to 1200 h; mid: 1200 to 1600 h; late: 1600 to 2000 h), sex, ontogenetic stage (adult or juvenile) and individual were added as independent variables in the relevant MANOVAs, and interactions between these variables and scent stimuli were assessed. I assessed correlations between behavioural activities using a Bonferroni-adjusted Spearman's correlation analysis. Subsequently, linear mixed effects (LME) models were used to perform detailed univariate ANOVAs for each behavioural activity (as dependent variables) to assess the relative importance of significant independent variables (from MANOVA) in determining behaviour. Individual was included as a random factor in these analyses to account for it as a source of variation (Sih *et al.* 2004, Stapley & Keogh 2004), as is necessary with the repeated measures experimental design.

I constructed a Wilks Lambda multivariate test to investigate whether the novel environment of the test arena influenced the behaviour of geckos and, if it did, whether successive conditioning trials reduced behavioural variation associated with the novel test environment. Individual and trial number were included as factors in the MANOVA. I compared a complete model (three levels of trial number) with reduced models (merged trial effects) using Wilks Lambda and approximate F tests, based on appropriate sums of squares and cross-products matrices.

4.4 Results

I detected no difference between behavioural responses of geckos to the negative control and the washing controls ($F_{(21, 51.1)} = 0.510$, p = 0.954), which confirms that the washing methodology was effective at removing scents. Significant behavioural variation was observed between the first conditioning trial and subsequent trials ($F_{21,63.72} = 3.615$, p < 0.001). I detected no behavioural differences between the second and third conditioning trial ($F_{21,63.72} = 1.454$, p = 0.128), suggesting that the novel test environment influenced behaviour during the first conditioning trial only. My methodology involving three conditioning trials prior to experimental trials therefore seems sufficient to minimise the influence of a novel environment on gecko behaviour, and is consistent with findings on the effects of conditioning prior to physiological experiments in this species (Hare *et al.* 2004).

Cologne (the positive control in this experiment) induced geckos to elevate their rate of tongue flicking ($t_{48} = 2.266$, p = 0.028) and increase overall activity ($t_{48} = 2.082$, p = 0.043), but other behavioural activities were not affected (p > 0.05 for all). Encountering a novel scent stimulus therefore results in a greater vomerolfactory response in *N. manukanus*, and greater exploratory behaviour, but does not alter other

components of behaviour. The observed response to the positive control demonstrates that my experimental protocol is valid for this species, and it sets a standard from which to explore recognition of fruit, conspecific and predator scents.

Rate of tongue flicking in *N. manukanus*, averaged across all scent stimuli, was 2.75 ± 0.13 tongue flicks per minute (range 0.08 to 6.42). Geckos spent almost half (45.8 %) of time during trials motionless, though this varied according to the scent stimulus presented (Fig. 1). The most common activity (34.1 % of time) was climbing, followed by movements of head, limbs or tail (8.2 %), nudging the wall (7.2 %) and slow walking (4.7 %; Fig. 1). Not surprisingly, climbing was negatively associated with slow walking, movements of head, limbs or tail, and freeze behaviour (Table 1). Exploratory slow walking was positively correlated with tongue flicking rate and movements of head, limbs or tail (Table 1). Geckos seldom exhibited a flight response; running accounted for less than 0.1 % of time (Fig. 1).

Adult *N. manukanus* responded to the chemical cues of fruit, conspecifics and native predators ($F_{(35, 166.49)} = 2.425$, p < 0.001). Individual variation in behaviour was highly significant ($F_{(112, 261.8)} = 2.809$, p < 0.001). The only intersexual difference in behavioural patterns observed ($F_{(7, 39)} = 3.419$, p = 0.006) was that females spent more time in slow, deliberate walking behaviour than males ($t_{16} = 2.934$, p = 0.010). Although pregnancy can affect chemosensory-mediated behaviour in geckos, it is expected to decrease mobility (Downes & Bauwens 2002), therefore I suggest that reproductive condition of female *N. manukanus* did not dramatically influence their behaviour which is consistent with findings from *H. maculatus* (Chapter 5). I observed sex-specific responses to the scent stimuli ($F_{(35, 166.49)} = 1.587$, p = 0.029). Temperature and time of trial did not influence behaviour ($F_{(7, 39)} = 0.780$, p = 0.608 and $F_{(14, 78)} = 1.213$, p = 0.284, respectively).

The scent of fruit elicited more climbing behaviour ($t_{48} = 2.565$, p = 0.014; Fig. 2) and a decrease in two correlated behaviours (Table 1): slow, deliberate walking ($t_{48} = -3.329$, p = 0.002) and time spent motionless ($t_{48} = -2.174$, p = 0.037). Males spent more time in slow, deliberate walking behaviour in response to the scent of fruit than females ($t_{48} = 3.020$, p = 0.004).



Figure 1. Activity of adult *Naultinus manukanus* when presented with no scent (i.e., a negative control; a) compared with the scent of fruit (b), a conspecific gecko (c), and faeces of a native reptilian predator (tuatara, *Sphenodon punctatus*; d).

Table 1. Correlations between activities and actions of Marlborough green geckos, *Naultinus manukanus*, and their significance based on Bonferroniadjusted Spearman's correlation analysis. Positive Spearman's coefficients indicate positive associations (i.e., an increased likelihood of one behaviour increasing the likelihood of another). Significant correlations (p < 0.05) are shown in bold. * 'move' refers to non-directional movements of the head, limbs and tail; see Methods for definitions of behaviours.

	Activity or action									
	Slow walk	Run	Move*	Freeze	Nudge wall	Climb	Tongue flick			
Run	-0.0835									
Move*	0.3995	0.0300								
Freeze	0.1061	0.0134	0.1501							
Nudge wall	0.1520	-0.0798	-0.2095	-0.0468						
Climb	-0.3706	0.0147	-0.3772	-0.8971	-0.2511					
Tongue flick	0.4432	-0.1775	0.3323	0.2406	0.1182	-0.3886				
Eye lick	-0.1435	-0.0389	0.1432	0.3354	-0.2711	-0.2197	0.0916			



Figure 2. Behavioural responses of *Naultinus manukanus* to the scent of fruit (pear; a & b), conspecific geckos of the opposite sex (c & d) and faeces of a native reptilian predator (tuatara, *Sphenodon punctatus*; e & f). Despite (a) the lack of vomerolfactory response to pear scent, as measured by tongue flicking, geckos showed (b) increased exploratory activity, as indicated by time spent climbing. Male geckos increase both (c) rate of tongue flicking and (d) exploratory activity, as measured by slow, walking behaviour in response to the scent of conspecific females. Geckos show reduced activity including (e) decreased lingual sampling of the substrate and (f) an increased tendency to remain motionless in response to tuatara faecal cues. Females are represented by filled circles; males are represented by open squares. Individual variation in behaviour is accounted for, and corrected estimates of behaviour are presented ± 1 standard error.

Conspecific scent induced male geckos to elevate their rate of tongue flicking to a greater extent than females ($t_{48} = 2.827$, p = 0.007; Fig. 2). An increase in slow, deliberate walking behaviour by males in response to the scent of conspecifics was also detected ($t_{48} = 2.326$, p = 0.024; Fig. 2). These activities are correlated (Table 1).

The response of adult geckos to native predator (tuatara) scent was dependent upon the cue provided. Tuatara skin secretions elicited only a higher rate of eye licking ($t_{48} = 2.889$, p = 0.006), but their faeces reduced both tongue flicking ($t_{48} = -2.205$, p = 0.032; Fig. 2) and slow, deliberate walking ($t_{48} = -3.431$, p = 0.001), which are correlated behaviours (Table 1). Tuatara faecal cues also induced increased freeze behaviour by geckos ($t_{48} = 2.106$, p = 0.040; Fig. 2). The apparently disproportionate reduction in tongue flicking by females compared with males in response to tuatara scent (Fig. 2) is not significant ($t_{48} = 1.857$, p = 0.070). Juveniles and adults responded similarly to faecal cues of tuatara; I detected no interaction between ontogenetic stage and scent stimuli ($F_{(7, 11)} = 1.443$, p = 0.281). However, adults showed reduced activity ($t_{17} = -2.217$, p = 0.041) and exploratory behaviour (nudging walls; $t_{17} = -3.387$, p = 0.004) relative to juveniles, demonstrating overall ontogenetic differences in behaviour.

4.5 Discussion

The observed behavioural responses of *N. manukanus* to the scent of fruit, conspecifics and native predators demonstrate chemosensory recognition of a variety of chemical cues and the ability to respond accordingly. Despite a different suite of selective pressures relative to the global norm and an outwardly visual strategy, diurnal New Zealand geckos do not appear to have reduced chemosensory abilities or exhibit the visual-chemosensory trade off seen in agamids and chameleonids.

Naultinus manukanus respond to the scent of fruit by spending more time exploring, as indicated by increased climbing activity and decreased freeze behaviour, as predicted. This behavioural response implies recognition of the stimulus and may represent an attempt to locate the fruit. Because this behavioural response was not accompanied by a change in frequency of lingual sampling, it is possible that the behaviours were elicited primarily by olfactory cues rather than vomerolfactory cues (Cooper & Pèrez-Mellado 2001). Although New Zealand lizards are primarily insectivorous, frequent observations of lizards consuming fruit in nature (Whitaker 1987, Wotton 2002), and an increased capture rate of lizards in traps baited with fruit (Whitaker 1967), imply a role for chemoreception in the location of food sources. Congeneric diurnal geckos, N. gravi, in New Zealand feed both on manuka, Leptospermum scoparium, nectar and dodder laurel, Cassytha panicula, while reports of frugivory and nectivory in nocturnal geckos, *Hoplodactylus* spp. are numerous (Whitaker 1987, Wotton 2002). I confirm the use of chemoreception to recognise fruit in *N. manukanus*, which supports the hypothesis that New Zealand lizards actively seek nectar and fruit, and may have played an important role in the evolution of plant reproductive strategies, proposed by Whitaker (1987). Diurnal geckos in other parts of the world also interact with flowering plants (Murphy & Myers 1996, Nyhagen et al. 2001). For example, the Mauritian ornate day gecko, *Phelsuma ornata ornata*, frequently consumes nectar and occasionally pollen, preferring flowering trees to fruiting trees, and visiting up to 80% of all plant species in the ecosystem (Staub 1988, Nyhagen et al. 2001). My results support the recent hypothesis that location of fruit using chemical cues is widespread among omnivorous and herbivorous reptiles (Cooper et al. 2001).

A sex-specific vomerolfactory and behavioural response to conspecific scent in *N*. *manukanus* suggests that chemoreception mediates intraspecific interactions. Males responded to female scent by increasing their rate of tongue flicking and employing slow, stalking movements characteristic of normal, exploratory behaviour in this species. Females did not appear to respond to male scent. The elevated tongue-flicking rate of *N. manukanus* males in response to female scent is also observed in other lizard species. For example, the rate of lingual sampling by the lizard *Podarcis hispanica* is greater in response to non-gravid than gravid females and to conspecific than heterospecific females (Cooper & Pèrez-Mellado 2002). The male response to female scent may indicate that males take the active role in mate searching. However, investigating whether these geckos produce chemical secretions in different seasons and use scent marks on the substrate is necessary for interpreting the use of chemosensory cues in mediating conspecific interactions.

Naultinus manukanus displayed an antipredator response to faecal cues produced by native tuatara, but not to their skin secretions. Tuatara are primarily nocturnal, generalist predators that are known to include nocturnal geckos (*Hoplodactylus* spp) in their diet, but I have found no reports of their predation of *Naultinus* geckos (Walls 1981). However, diurnal *Naultinus* geckos share vine and ground habitats with tuatara on Stephens Island, and although tuatara are primarily nocturnal, activity during the day is common (pers. obs.). Tuatara faecal cues reduced activity and exploratory behaviour in both adult and juvenile geckos, suggesting that chemosensory predator recognition is innate and that chemosensory cues alone are sufficient to prompt an antipredator response. Tuatara are medium-sized reptiles capable of eating even an adult gecko, so the similarity in antipredator response irrespective of ontogenetic stage is to be expected (but see Head *et al.* 2002). Decreasing activity in response to tuatara chemical signals may reflect an antipredator freeze response appropriate to this primarily visual, sit-andwait predator (Meyer-Rochow & Teh 1991). Behavioural responses of geckos to tuatara scent were not accompanied by an elevated rate of tongue flicking. The decreased tongue flicking rate might also represent an antipredator freeze strategy after detecting tuatara with the first tongue flick, or may indicate reliance on predator detection by olfactory recognition of volatile chemicals, rather then lingual sampling and vomerolfaction (Cooper 1995a, 1995b). However, as other native lizards (common geckos, *Hoplodactylus maculatus*, and common skinks, *Oligosoma nigriplantare polychroma*) do not show an antipredator response to tuatara urine and faeces (Chapter 5), implications of this finding must be treated cautiously.

Antipredator freeze responses, mediated by chemoreception, function to increase survival of the Australian skinks, *Lampropholis guichenoti*, when in the vicinity of snake, *Demansia psammophis*, predators (Downes 2002). By decreasing activity and mobility, these skinks evade detection by snakes. The same behavioural tendencies of geckos in response to predatory tuatara scent is indicative of freeze responses to sit-and-wait predators which are common among reptilian prey (Greene 1988).

Evolution under a reduced suite of selection pressures, resulting from 80 my of isolation from mammalian and snake predators, seems not to have decreased chemosensory capabilities of New Zealand's apparently visual-oriented, diurnal geckos. I find no evidence for a functional loss of chemosensory capabilities associated with evolution of primarily visual life history strategies in non-iguanid squamates; this contrasts with the secondarily reduced chemosensory abilities seen in agamids and chameleonids (Schwenk 1993). Instead, chemosensory capabilities consistent with other squamates have been retained by *N. manukanus*, and appear to play a functional role in their biotic interactions. My findings support the hypothesis that chemosensory traits remain highly conserved among squamates, reflecting suprafamilial attributes rather than local adaptation.

CHAPTER 5

Does evolution in isolation from mammalian predators have behavioural and chemosensory consequences?⁶

5.1 Abstract

Recently introduced mammalian predators have had devastating consequences for biotas of archipelagos that were isolated from mammals over evolutionary time. However, understanding of which antipredator mechanisms are lost through relaxed selection and how they influence the ability of prey to respond to novel predatory threats is limited. The varying effects of relatively recent mammalian introductions to New Zealand's islands on native lizard populations provide an opportunity to examine the consequences of relaxed selection. I assess behavioural patterns and predator detection abilities of native lizards, using chemicals of native reptilian and introduced rodent predators as cues. Focal lizard populations were isolated from predatory mammals for 10-80 my; some now coexist with mammals while others remain in mammal-free locations. Skinks that evolved with mammals and have recently been introduced to New Zealand are included for comparison. Lizard behavioural patterns were correlated with their experience of mammals. Lizards always isolated from mammals exhibited the most antipredator freeze behaviour, whereas those that coevolved with mammals exhibited greatest activity (movements). However, predator

⁶ Co-authors for publication: N.J. Nelson, C.H. Daugherty, D.H. Brunton and R. Shine

chemical cues did not induce specific antipredator responses in any species, indicating that these behavioural patterns are not linked to chemosensory predator detection alone.

5.2 Introduction

Evolutionary isolation from common predator guilds may lead to relaxed selection and the loss of costly antipredator traits and behaviours among prey species (Coss 1999, Magurran 1999, Blumstein 2002, Blumstein & Daniel 2005). Human-mediated dispersal of predators has often resulted in range contractions and extinctions of prey species that have been geographically isolated from these predators historically (Cassels 1984, Worthy & Holdaway 2002). Investigating how major classes of predators influence antipredator traits is essential to understanding why certain species are particularly vulnerable to novel predators (Bunin & Jamieson 1996, Blumstein 2002). Archipelagos that were evolutionarily isolated from mammals and to which mammals have recently been transported provide a powerful framework in which to test questions concerning the consequences of isolation from a predator guild. Lizards in New Zealand with varying histories of exposure to predatory mammals (Chapter 1) provide an opportunity to test the roles of coevolution and recent experience with mammals in determining behavioural patterns and predator detection abilities.

Endemic New Zealand reptiles have undergone a precipitous decline since the arrival of humans (Towns & Daugherty 1994). The decline is primarily attributed to predation by introduced mammals (e.g., Cassels 1984, Case & Bolger 1991). New Zealand reptiles did not encounter predatory mammals for ca. 80 my, prior to human contact 2000-1000 ya (Anderson 1996, Holdaway 1996). Islands never reached by mammals or from which mammals are removed often support high lizard densities (e.g., Daugherty *et al.* 1990c, Towns 1996; Chapter 3). For example, 41% of the 65 extant

endemic reptile species in New Zealand now survive largely or entirely on rat-free offshore islands (Towns & Daugherty 1994). In contrast, reptiles that coevolved with mammals have not proven so susceptible to invasive mammals (Gibbons *et al.* 2000).

Remarkably, research into exactly why the New Zealand herpetofauna is so susceptible to mammalian predation is scant. Predatory birds were diverse and abundant over the long period of New Zealand's isolation from other land masses (Worthy & Holdaway 2002), and the larger endemic reptiles were also a predatory threat for smaller lizards. Two hypotheses may explain the extreme vulnerability of New Zealand lizards to mammalian predation. Introduced mammals could represent:

- Additional predation pressure: the low reproductive outputs (delayed maturation, infrequent production of small clutches) of New Zealand reptiles associated with K-selected life history patterns in a cool temperate environment (Cree 1994) are easily disrupted by additional sources of mortality. Species-specific patterns of range restriction among New Zealand reptiles support this hypothesis, as the longer-lived (and generally larger) endemic lizards are disproportionately affected by mammal presence (Daugherty *et al.* 1993, Towns & Daugherty 1994; Chapter 2);
- Novel predation pressure: mammalian predation is different from, rather than simply additional to, bird predation (Blumstein 2002, Worthy & Holdaway 2002). The absence of selective pressure by mammalian predators may have rendered New Zealand lizards either less likely to detect and behaviourally respond to mammals, or easy for mammals to locate or to capture.

I investigate the second hypothesis by assessing lizard behaviours and chemosensory predator detection abilities according to their evolutionary and recent exposure to mammals.

New Zealand lizards coevolved with primarily visual native predatory birds and tuatara (Sphenodon spp; Meyer-Rochow 1988, Meyer-Rochow & Teh 1991, Worthy & Holdaway 2002). The visual crypsis and secretive behaviours exhibited by native lizards (e.g., Appendix 1) are presumably the results of strong selective pressure to avoid detection by native predators. However, this strategy may be unsuitable for avoidance of novel mammalian predators that hunt primarily using scent and have a speed advantage over ectothermic prey, particularly in cool temperate locations (Armsworth et al. 2005, Hare 2005). Chemosensory predator detection is common among squamate reptiles (Burghardt 1970, Cooper & Burghardt 1990), particularly to facilitate avoidance of snake predators (Downes & Shine 1998, Downes & Adams 2001, Amo et al. 2004). Chemosensory mechanisms used by lizards to avoid mammalian predators are poorly researched (Kats & Dill 1998; but see Cowles 1938). Endemic diurnal geckos, *Naultinus manukanus*, show some ability to detect strong (faecal) cues of native reptilian predators (tuatara; Chapter 4), suggesting that chemoreception may also play a role in antipredator behaviour of New Zealand lizards. However, the extent to which New Zealand lizards are able to detect and behaviourally respond to native and introduced predators using chemosensory cues is unknown. In the absence of nearly all terrestrial predators (exceptions being tuatara and some native flightless birds), selection on chemosensory abilities of New Zealand lizards may have been relaxed, resulting in their loss.

Groups of lizards in New Zealand provide an opportunity to investigate both behavioural and chemosensory consequences of evolution without selective pressure from mammalian predators: (1) native geckos and skinks evolved in isolation from mammalian predators (80 my for geckos, Chambers *et al.* 2001; 10-25 my for skinks, Daugherty *et al.* 1990b, Hickson *et al.* 2000), and (2) introduced skinks (rainbow skinks, *Lampropholis delicata*) coevolved with mammals in Australia and were probably introduced to New Zealand via cargo in the 1960s (Gill & Whitaker 1996).

Native lizards are located on the New Zealand mainland (North and South Islands) and offshore islands with different histories of exposure to mammals. Kiore, *Rattus exulans*, have been present on mainland New Zealand for up to 2000 y (Holdaway 1996), and another 30 species of mammals introduced by European settlers have established in the past ca. 200 y (King 2005), though a number of offshore islands remain mammal-free.

I investigate the ability of lizards to recognise chemicals of predatory tuatara, reptiles endemic to New Zealand, and ship rats, *R. rattus*, which established in the North Island after 1860 (King 2005). I test whether experience of, and evolution with, mammalian predators determines (1) behavioural patterns, and (2) chemosensory predator recognition abilities of lizard prey by addressing the following questions:

- Do predator detection abilities vary among species isolated from mammalian predators? I compare four lizard species on a mammal-free offshore island.
 Species were selected to encompass both skinks and geckos, and species that are now rare or common at locations where they now coexist with mammals.
- 2. Do behaviours and predator detection abilities vary within species according to recent exposure to mammalian predators? I compare populations of widespread and abundant native skinks and geckos from proximate geographic locations that are either affected by introduced mammals or mammal-free.
- 3. *Does coevolution with mammalian predators influence lizard behaviours and predator detection abilities?* I compare native skinks that were evolutionarily isolated from mammalian predators with introduced skinks that coevolved with mammals and snakes.

5.3 Methods

5.3.1 Study sites

Study sites comprised two North Island locations where introduced mammals are present, Pukerua Bay and Turakirae Head, and two mammal-free locations, North Brother Island (4 ha) and Stephens Island (150 ha) in adjacent Cook Strait (Fig. 1). The North Island sites are inhabited by a diverse range of introduced mammals, including rodents, mustelids and cats (King 2005). Mammals never reached North Brother Island. Cats were introduced to Stephens Island in the late 19th Century and spread quickly, but were eradicated by lighthouse keepers by 1925 (Brown 2000); the island has remained free of predatory mammals since 1925. Introduced skinks, which coevolved with mammalian predators as well as birds and reptiles, were collected from the Otara and Mount Wellington suburbs of Auckland, North Island (Fig. 1). They were accidentally introduced into New Zealand from Australia in the 1960s, probably via movement of cargo (Gill & Whitaker 1996), and are now well established in the northern North Island, though have not yet reached the Cook Strait region (Peace 2004). Under a pre-human predation regime, predators of native New Zealand lizards are predominantly birds, especially kingfishers, Halcyon sancta, ruru, Ninox novaeseelandiae, gulls, Larus spp., and Australasian harriers, Circus approximans, and larger reptiles, including tuatara (Whitaker 1972). After mammals were introduced to New Zealand, tuatara and some larger lizard species became extinct on the mainland and restricted to mammal-free outlying islands, such as North Brother and Stephens Islands. Thus, mammals (especially rodents, cats and mustelids; King 2005) have replaced larger reptiles as lizard predators throughout much of New Zealand. I assume that the intensity of bird predation is approximately equivalent at both mammal-affected and mammal-free sites.



Figure 1. Sampling localities for lizards. Common geckos, *Hoplodactylus maculatus*, and common skinks, *Oligosoma nigriplantare polychroma*, were collected from all sites marked in the Cook Strait region. The rare Marlborough green geckos, *Naultinus manukanus*, and speckled skinks, *O. infrapunctatum*, were collected from Stephens Island. Introduced rainbow skinks, *Lampropholis delicata*, were collected from Auckland (on the inset map of New Zealand). Mammals are present throughout the North Island of New Zealand. Stephens and North Brother Islands are mammal-free.

5.3.2 Study species

Behaviours of the widespread and abundant common skinks, *Oligosoma nigriplantare polychroma*, and common geckos, *Hoplodactylus maculatus*, sourced from mammal-free Stephens Island were compared with those of sympatric populations of rare, speckled skinks, *O. infrapunctatum*, and Marlborough green geckos, *N. manukanus*. The New Zealand threat classification system ranks speckled skinks as in "gradual decline" and Marlborough green geckos as "sparse" due to human activities (Hitchmough 2002). Common skinks and common geckos were collected from all Cook Strait sites, encompassing mammal-free and mammal-affected sites, to investigate intraspecific variation in behaviours and predator detection abilities. Introduced rainbow skinks, *Lampropholis delicata*, were used as an out-group that coevolved with mammals and compared with common skinks. Rainbow skinks can use chemosensory cues to respond to snake predators in their native range (Downes & Hoefer 2004).

Common geckos and common skinks were captured through pitfall trapping and hand searching between November 2003 and May 2005 (see Table 1 for capture dates and sample sizes). Lizards from the less common species, Marlborough green geckos and speckled skinks, were also captured on Stephens Island in November 2003 (Table 1). Additionally, introduced rainbow skinks were captured in Auckland in October 2005 (Table 1). Although seasonal differences in sampling were unavoidable, samples from within each treatment were spread across the seasons, and the inactive phase during winter months was avoided (Table 1). Sex was determined by external examination (geckos) or hemipene eversion (skinks), reproductive condition of females was assessed by palpation, and snout-vent length (to 1 mm) and mass (to 0.1 g for lizards < 30 g, and 0.5 g for lizards \geq 30 g) were measured. Lizards captured on Stephens and North Brother Island were held temporarily in captivity on the respective islands for behavioural trials, whereas those from Pukerua Bay and Turakirae Head

Table 1. Capture information for native geckos *Hoplodactylus maculatus* (Hm) and *Naultinus manukanus* (Nm), and skinks *Oligsoma nigriplantare polychroma* (Onp) and *O. infrapunctatum* (Oi) and introduced *Lampropholis delicata* (Ld) used in behavioural experiments. Snout-vent length (SVL) is recorded to the nearest 1 mm. Mass is recorded to 0.5 g for lizards \geq 30 g and to 0.1 g for lizards < 30 g.

Species	Abundance	Site	Predation regime	N	2	♀ (P/G) ^a	Capture dates	SVL (mm)	Mass (g)
Hm	common	Stephens Is.	Natural	30	13	17 (13)	3-16 Nov. 2003	55-75	3.5-10.5
Hm	common	North Brother Is.	Natural	30	12	18 (6)	23-29 Feb. 2004	65-80	7.0-12.0
Hm	common	Pukerua Bay	Modified	29 ^b	12	17 (0)	3 Feb. – 23 Apr. 2004	63-75	5.0-9.5
Hm	common	Turakirae Head	Modified	30	19	11 (0)	17 Apr. 2005	52-66	2.5-7.5
Onp	common	Stephens Is.	Natural	9	6	3 (1)	10-20 Nov. 2003	50-66	2.0-5.1
Onp	common	North Brother Is.	Natural	30	10	20 (0)	24-27 Feb. 2004	55-68	2.5-5.0
Onp	common	Pukerua Bay	Modified	30	17	13 (0)	2 Feb. – 17 Mar. 2004	53-65	2.3-4.5
Onp	common	Turakirae Head	Modified	6	2	4 (0)	17 Apr. – 31 May 2005	47-62	1.7-3.6
Nm	rare	Stephens Is.	Natural	30	15	15 (13)	3-16 Nov. 2003	44-76	3.2-11.0
Oi	rare	Stephens Is.	Natural	30	7	23 (20)	5-19 Nov. 2003	76-116	10.0-33.0
Ld	invasive	Auckland	NA	25	12	13 (1)	10 Oct. 2005	35-47	0.7-1.9

^aP = pregnant, G = gravid; ^b10 of 29 *H. maculatus* at Pukerua Bay were trialled at night, during their activity phase (see methods).

were held at Victoria University of Wellington (VUW), and rainbow skinks from Auckland were held at the Albany campus of Massey University (MU).

All lizards were kept individually in 2 L plastic containers with 1 x 1 mm wire mesh (165 x 120 mm) in the lid for ventilation and to enable basking. Food and water were supplied *ad libitum*, the food consisting of mealworm larvae (*Tenebrio molitor*) and/or pureed pear. On the two islands, lizards were kept under natural light and temperature (9.0 to 26.3°C) conditions; at VUW temperature of the room ranged from (13.6 to 22.6°C), and photoperiod was on a 12:12 light:dark cycle (on at 0600 h); at MU skinks were kept under natural light and temperature (16.7 to 23.2°C) conditions.

5.3.3 Experimental procedure

My experimental methodology for testing prey responsiveness to predator chemical cues is adapted from Downes and Shine (1998), and has proven successful for evoking antipredator responses in both Australian and native geckos (Downes & Shine 1998; Chapter 4). Experimental methodology follows the same procedures used for adult *N. manukanus* described in Chapter 4; brief methods and differences are explained here. Calico cloth covering the base of the experimental arena was treated in one of four ways, after being thoroughly washed (Chapter 4): (1) negative control: no scent; (2) positive (chemical pungency) control: calico was sprayed with commercial cologne ('Smiley') and air-dried, (3) tuatara scent: calico was sprayed with a solution of tuatara urine and faeces (4) rat scent: calico was sprayed with a solution of ship rat urine and faeces.

Samples were collected from both captive (at VUW) and wild-caught (from Stephens and North Brother Islands) tuatara and captive rats (from Nga Manu Nature Reserve). Ship rats are known predators of common geckos (Chapter 2), and likely predators of other New Zealand lizards. A current debate over the diet of predators influencing responsiveness of prey (e.g., Nolte *et al.* 1994, Murray *et al.* 2004 Wirsing *et al.* 2005) led me to take a cautious approach to feeding of predators whose urine and faeces were used as the chemical cues in experiments of lizard responsiveness. I fed captive tuatara and rats neutral diets of invertebrates and/or grains, and never lizards. Wild-caught tuatara may have consumed lizards; gecko and skink remains are both found in ca. 3% of tuatara scats on Stephens Island (Walls 1981).

Behaviour of lizards was observed continuously for 8 min periods using an observational data logging programme that I created in collaboration with Edwin Hermann, Victoria University of Wellington ('AnimalSpy', version 1.1.0) to record behaviour directly onto the computer. Prey animals may exhibit a suite of behavioural responses following exposure to predators, including direct displacement and alterations in movement or activity patterns (e.g., Lima & Dill 1990). For example, lizard avoidance of mammalian predators can take a variety of forms, including running, remaining motionless, vibrating the tail laterally against the substrate, defecating and/or vocalising (Daniels *et al.* 1986). In contrast, I expect normal maintenance behaviour of lizards to include a greater proportion of slow, stalking walk behaviour and snout licking. I therefore chose to measure a variety of behaviours. The relative proportions of these behaviours were used to indicate responsiveness to chemical stimuli. Either the duration (in seconds; 1 to 10) or the frequency (11 and 12) of the following spatial use, behavioural and locomotor acts was recorded:

- On cloth: the lizard is on the test substrate placed on the base of the enclosure (no more than one foot is off the horizontal surface);
- (2) On wall: all four feet are on the vertical surface;
- (3) Stand up: two or three feet are on the vertical surface (i.e., the lizard is using the enclosure base to stand against the wall);

- (4) Slow walk: the lizard proceeds by very slow, stalking movements of the limbs on the horizontal surface;
- (5) Walk: the lizard proceeds by continuous movements of the limbs on the horizontal surface;
- (6) Run: very fast movement on the horizontal surface;
- (7) Climb: the lizard proceeds by movement of the limbs on the vertical surfaces (rarely observed in skinks);
- (8) Nudge wall: repeated pressing of head against vertical surface of enclosure;
- (9) Stationary, moving head, limbs or tail: the lizard moves body parts but does not alter its position in the enclosure;
- (10) Stationary, freeze (i.e., motionless): no movement of any body part;
- (11) Tongue flick: the lizard extrudes its tongue and it either waves in the air, or is rapidly lowered to touch the substrate;
- (12) Snout lick: the lizard extrudes its tongue and raises it to lick the nostrils or snout, before being retracted.

Location of the lizard in the test arena (1-3) and behavioural/locomotory acts (4-

10) were recorded continuously throughout the behavioural trial. Instantaneous actions (11-12) were recorded as count data when they occurred. Chemosensory-mediated antipredator responses could take one of two major forms: (1) an increase in freeze behaviour and decrease in activity, or (2) an increase in escape activity, including running, walking, climbing or nudging the wall. I would expect either response to be accompanied by an increase in vomerolfactory sampling (as measured by tongue flicking rate) and decreased maintenance behaviour (slow walking, non-directional movement of head, limbs and tail, and snout-licking).

Lizards were conditioned to experimental procedures (using the methodology outlined in Chapter 4) to minimise the effect of a novel environment on behaviour (Blumstein *et al.* 2002, Hare *et al.* 2004). Conditioning for a minimum of one trial has proven effective for this type of experiment for *N. manukanus* (Chapter 4). Each native lizard performed each of the four scent tests in a randomly selected order, and performed a maximum of one trial per day. Introduced rainbow skinks were trialled with only rat scent and controls, as tuatara scent was not considered ecologically relevant to them. Ambient temperature was measured at the start of each trial and included in analyses.

5.3.4 Statistical analyses

Data were analysed in the statistical programme 'R' (version 2.3.1). Continuous data (lizard position and activity) were converted to proportions of total time spent in each activity and square roots of count data (tongue flicks and snout licks) were taken for analyses.

(1) Native common skink and common gecko intraspecific comparisons: Initially, multivariate analyses of variance (MANOVAs), using the F approximation to the Wilks test, were performed to assess (1) reproductive condition of females (as it influences behaviour in some lizard species; Downes & Bauwens 2002), and (2) time of trial (day or night), in explaining variation in behavioural acts (the dependent variables). Datasets for these tests comprised: (1) female common geckos from Stephens Island and North Brother Island, in which a subset of females were pregnant during behavioural tests (sample sizes in Table 1), and (2) common geckos from Pukerua Bay, 10 of which were trialled during the night (i.e., during their activity phase), and 19 during the day. Scent, individual and temperature were included as factors in both analyses. An interaction term between scent and the factor being tested (reproductive condition and day/night trial, respectively) was also included. Additionally, site was included as a factor when testing for the significance of pregnancy, and sex was

included when testing the influence of activity phase. Linear mixed effects models were used to obtain more information where significant results were found.

A MANOVA was also used to assess the overall importance of presence or absence of introduced mammals at sites, scent, species, temperature, the site and individual variation on behaviour. All data were used in this analysis, after excluding geckos trialled at night (see Results). As species-specific behavioural differences were found (gecko or skink; $F_{10,505} = 229.5$, p < 0.001), separate MANOVAs including the same factors were performed for each species. I also assessed correlations between behavioural activities using a Bonferroni-adjusted Spearman's correlation analysis.

Species-specific linear mixed effects (LME) models were then used to seek more detail about sources of behavioural variation. In these models, the presence or absence of mammalian predators, the scent stimulus, ambient temperature and site were tested as main effects, combined as interaction terms, and compared against a null model. Individual was included as a random effect in all models. The model which best predicted lizard behaviour was chosen using Akaike's Information Criteria (AIC; Akaike 1973, Burnham & Anderson 1998), and significance of model components was verified using univariate ANOVAs. Site is nested within the presence or absence of mammals (predation regime) and includes more detail. However, if site is selected in the best AIC model it does not exclude attributing variance to the predation regime.

(2) **Interspecific comparisons:** I compared the responses of rare versus common lizards (geckos and skinks, in separate analyses) to scent stimuli using MANOVAs which included individual, temperature, scent stimulus and an interaction between scent stimulus and species as factors. Responses of New Zealand common skinks and introduced Australian rainbow skinks were compared in a MANOVA with the same fixed factors, though using predation history instead of species, to separate common skink populations according to exposure to mammals. Univariate LME models were used to seek more detail on behavioural differences between common and rainbow skinks; these included significant factors from the MANOVA.

5.4 Results

5.4.1 Do predator detection abilities vary among species isolated from mammalian predators?

Under a natural predation regime, on mammal-free Stephens Island, I found no interspecific variation in chemosensory predator recognition abilities of either skinks or geckos according to whether a species was rare or common (Table 2). Results presented from here on therefore pertain to common skinks and geckos, unless otherwise stated.

5.4.2 Do behaviours and predator detection abilities vary within species according to recent exposure to mammalian predators?

Reproductive condition of female lizards did not alter their overall behaviour $(F_{10,120} = 1.261, p = 0.256)$ or response to scent stimuli $(F_{30,352.9} = 1.269, p = 0.266)$. I therefore pooled pregnant and non-pregnant female lizards in further tests. Time of trial (day-night) influenced behaviour of primarily nocturnal common geckos $(F_{10,91} = 7.729, p < 0.001)$. Geckos showed a greater tendency to climb $(t_{27} = 2.406, p = 0.023)$ and spent less time motionless $(t_{27} = -3.272, p = 0.003)$ during their active phase at night. Only geckos that were trialled during daylight hours were included in further analyses, even though responses to scent stimuli did not differ according to time of trial $(F_{30,191.46} = 0.647, p = 0.921)$.

Table 2. Summary of hypotheses, experiments and results for the factors influencing behaviour of New Zealand lizards, which were isolated from predatory mammals over evolutionary time (80 my). Widespread and abundant endemic geckos, *Hoplodactylus maculatus*, and skinks, *Oligosoma nigriplantare polychroma*, from mammal-free sites and those affected by introduced mammals were used in the main experimental design. Range restricted and relatively rare endemic geckos, *Naultinus manukanus*, and skinks, *O. infrapunctatum*, were used for comparative purposes. The invasive Australian skink, *Lampropholis delicata*, was used as an out-group. Sample sizes are provided in Table 1.

Hypothesis	Experiment(s)	Results
A. Lizards recognise and behaviourally respond to predator scents	I presented individual <i>H. maculatus</i> and <i>O. n. polychroma</i> with predator chemical cues and positive and negative controls	Geckos responded to predator scent (MANOVA: $p = 0.0094$), but skinks did not ($p = 0.2655$)
B. Exposure to predatory mammals influences lizard behaviours	I compared behaviours of <i>H. maculatus</i> and <i>O. n. polychroma</i> collected from two mammal-affected sites and two mammal-free sites	Behaviours of geckos and skinks were correlated with the presence of mammals (MANOVA: $p < 0.0001$ for both). Exposure to mammals induced greater activity and less antipredator freeze behaviour (Fig. 3 & 4).
C. Lizards exposed to mammals show a greater response to predator chemical cues	I compared responses of <i>H. maculatus</i> (see Hypothesis A) collected from mammal-free vs. mammal-affected sites to predator cues and controls	Exposure to mammals did not influence responses to predator chemical cues (ANOVA: $p > 0.05$ for all)
D. Ability to recognise predator chemical cues enables lizards to coexist with predatory mammals	I compared responses of rare <i>N. manukanus</i> vs. common <i>H. maculatus</i> and rare <i>O. infrapunctatum</i> vs. common <i>O. n. polychroma</i> to predator chemical cues	Rarity is not correlated with response to predator chemical cues (MANOVA: $p > 0.5$ for both)
E. Lizards that co-evolved with predatory mammals are more able to recognise predator chemical cues	I compared responses of introduced <i>L. delicata</i> vs. native <i>O. n. polychroma</i> to predator chemical cues	Introduced and native skinks responded differently to chemical cues (MANOVA: $p = 0.0001$); introduced skinks elevated tongue flicking and movements of head, tail and limbs in response to novel and rat cues (ANOVAs: $p < 0.05$; Fig. 5)
F. Co-evolution with mammals results in greater lizard activity	I compared behaviours of introduced <i>L. delicata</i> vs. native <i>O. n. polychroma</i>	Introduced skinks were more active than native skinks; they spent more time slow walking, walking and nudging wall, and less time motionless (ANOVAs: $p < 0.05$ for all)

Geckos were more active than skinks during trials, spending, on average 43% of time moving about the enclosure, compared with 21% of time by skinks (trials from all sites pooled using only a negative scent control; Fig. 2). Running by either skinks or geckos was infrequently observed, and skinks seldom walked (Fig. 2); significant variation in these activities was therefore treated with caution. Unsurprisingly, geckos also spent more time climbing on the walls of the enclosure. Rate of tongue flicking of skinks was twice that of geckos, but skinks did not exhibit the maintenance behaviour of snout licking, which averaged 5 licks per 8 min trial in geckos (Fig. 2).

Negative correlations between some activities and locations in the test arena are a function of the experimental design, as performing one activity eliminates the option of performing another (Table 3). However, positive correlations between activities, and any correlations between actions (tongue flicking and snout licking) and activities imply behavioural associations. Direction and significance of behavioural correlations are similar for skinks and geckos (Table 3). Of particular note are the positive associations between tongue flicking and exploratory behaviours (nudging the wall and non-directional movements), while tongue flicking is negatively associated with freeze behaviour (Table 3). Exploratory behaviours (nudging wall, slow walking and walking) are also consistently positively correlated (Table 3).

Common skink behaviour was not related to the scent stimulus presented ($F_{30,760,89}$ = 0.767, *p* = 0.811), so scent was excluded from detailed univariate models. Behavioural variation among common skinks was attributable to the presence or absence of mammals ($F_{10,259}$ = 12.862, *p* < 0.001), the site ($F_{10,518}$ = 2.194, *p* = 0.002), and the ambient temperature ($F_{10,259}$ = 5.310, *p* < 0.001), and sex ($F_{10,259}$ = 2.261, *p* = 0.015) though no specific behavioural activity was correlated with temperature or sex.



Figure 2. Position in the test arena, activities and actions of common geckos, *Hoplodactylus maculatus* (a, b & c, respectively) and common skinks, *Oligosoma nigriplantare polychroma* (d, e & f) during negative control trials, averaged across individuals from all sites.

Table 3. Correlations between activities and actions of common geckos, *Hoplodactylus maculatus* (normal text), and common skinks, *Oligosoma nigriplantare polychroma* (italics), and their significance based on Bonferroni-adjusted Spearman's correlation analysis. Positive Spearman's coefficients indicate positive associations. Significant correlations (p < 0.05) are shown in bold.

	On cloth	On wall	Stand up	Slow walk	Walk	Run	Climb	Nudge wall	Move ^a	Freeze	Tongue flick	Snout lick
On cloth		-0.3153	-0.9905	0.1399	0.0794	0.0541	-0.0174	0.0487	-0.0480	-0.0328	-0.0103	-0.2423 ^b
On wall	-0.8640		0.1818	-0.0629	-0.0053	-0.0227	0.1579	-0.0353	0.0233	0.0157	-0.0368	-0.0174
Stand up	-0.3741	-0.1437		-0.1358	-0.0815	-0.0528	-0.0050	-0.0453	0.0464	0.0317	0.0160	0.2536 ^b
Slow walk	0.3708	-0.3087	-0.1603		0.1379	0.1104	0.0631	0.6330	0.5885	-0.8260	0.6612	-0.0189
Walk	0.1313	-0.1531	0.0240	-0.0082		0.1179	0.1593	0.4171	0.1809	-0.3001	0.1302	-0.0537
Run	0.0575	-0.0807	0.0359	-0.1695	0.1457		-0.0244	0.1152	0.0233	-0.0857	-0.0535	0.1601
Climb	-0.6632	0.6571	0.0930	-0.1867	-0.0412	-0.0728		0.0217	0.0519	-0.0648	0.0963	-0.0034
Nudge wall	0.1659	-0.1793	0.0039	0.3813	0.2932	0.0283	-0.0207		0.5268	-0.7869	0.4807	0.0169
Move ^a	-0.3953	0.2440	0.3274	0.0708	0.0684	-0.0878	0.2554	0.0707		-0.9046	0.7877	0.0240
Freeze	0.1399	-0.0793	-0.1287	-0.5587	-0.2895	0.0803	-0.3236	-0.7013	-0.6329		-0.7917	-0.0105
Tongue flick	0.0159	0.0140	-0.0570	0.3359	-0.0636	-0.1122	0.0834	-0.0631	0.2885	-0.2582		0.0504
Snout lick	0.1014	-0.0753	-0.0605	0.1389	0.0289	-0.0669	-0.1004	0.0163	0.0753	-0.0733	0.2648	

^a'move' refers to non-directional movements of the head, limbs and tail; see Methods for definitions of behaviours; ^bAction was rarely performed so interpretation requires caution
Site-specific differences in skink behaviours (Table 4) were primarily attributable to the presence or absence of mammals at a site (Fig. 3). Skinks from the two sites where mammals are present, Pukerua Bay and Turakirae Head, showed a greater tendency to stand up against the walls of the test enclosure (Fig. 3a), rather than using its base, relative to those from the mammal-free locations. Skinks from the same mammal-affected populations also showed a tendency to be more active during trials: they spent a greater amount of time walking (Fig. 3b), nudging the wall of the test enclosure and moving head and limbs. These exploratory behaviours are positively correlated (Table 3). Conversely, skinks from locations in which mammals are present spent less time motionless than those from mammal-free locations (Fig. 3c). More lingual sampling of the substrate was conducted by skinks from locations where mammals are present (Fig. 3d).

In contrast to skinks, behavioural variation among gecko populations was attributable to the scent stimulus presented ($F_{30,1180.6} = 1.722$, p = 0.009), as well as the presence or absence of mammalian predators ($F_{10,402} = 29.879$, p < 0.001), the site from which they were sourced ($F_{20,804} = 9.121$, p < 0.001) and ambient temperature ($F_{10,402} = 19.306$, p < 0.001). Behaviours of adult geckos were not related to sex. Higher temperatures induced greater lingual sampling ($t_{311} = 2.400$, p = 0.017), particularly among geckos from sites where mammals were present ($t_{311} = 6.260$, p < 0.001). Additionally, higher temperatures during experiments resulted in geckos spending less time on the base of the test arena ($t_{309} = -2.024$, p = 0.044).

My finding that the scent stimuli presented to geckos influenced their positions within enclosures (Table 4) was driven primarily by cologne (the positive control) inducing geckos to spend more time on the enclosure walls and less on the scent cloth than either a negative control or predator chemical cues (Fig. 4). Tuatara (native predator) chemical cues produced a similar, yet weaker, response. Scent-induced

Hoplodactylus maculatus					Oligosoma nigriplantare polychroma			
Behavioural act	Predictor(s)	F value	df	р	Predictor(s)	F value	df	р
On cloth	scent	3.486	3, 309	0.016	site	20.578	3, 70	< 0.001
	temp	4.098	1, 309	0.044				
On wall	scent	2.963	3, 310	0.032	predator regime ^a	8.032	1, 72	0.006
Stand up	scent	3.895	3, 310	0.009	site	21.603	3, 70	< 0.001
Slow walk	site	3.287	3, 105	0.024	site	5.903	3, 70	0.001
Walk	site	19.717	3, 105	< 0.001	site ^a	12.378	3, 70	< 0.001
Run	predator regime ^a	8.521	1, 107	0.004	null	-	-	-
	scent ^a	2.996	3, 310	0.031				
Climb	scent	4.385	3, 310	0.005	null	-	-	-
Nudge wall	site	4.477	3,105	0.005	site	7.375	3, 70	< 0.001
Moving but not travelling	site	15.529	3, 105	< 0.001	site	8.690	3, 70	< 0.001
	scent	6.411	3, 310	< 0.001				
Motionless	null	-	-	-	site	8.690	3, 70	< 0.001
Tongue flicking	predator regime	18.847	1, 107	< 0.001	site	5.450	3, 70	0.002
	temp	31.287	3, 311	< 0.001				
	predator regime*temp	39.190	3, 311	< 0.001				
Snout licking	site	33.832	3, 105	< 0.001	null	-	-	-
	site *scent	3.603	12, 301	< 0.001				

Table 4. Results of model selection to determine the most significant predictors of lizard behaviour. '*' represents an interaction term.

^aThese results must be treated with caution, as the behaviours were rarely performed (Fig. 2).



Figure 3. Behavioural actions of common skinks, *Oligosoma nigriplantare polychroma*, during all scent trials (pooled) at each site. Behavioural actions portrayed are time spent: (a) standing against wall, (b) walking, and (c) motionless, and (d) lingual sampling of the substrate. Significant differences between populations sourced from mammal-affected sites (Pukerua Bay (PB) and Turakirae Head (TH)) compared with those from mammal-free sites (North Brother Island (NBI) and Stephens Island (SI)), were found for each of the behavioural actions shown (Table 4).

differences in behavioural activities were attributable to rat (introduced predator) cues triggering a running response (though geckos rarely ran; Fig. 4a), and both the positive control and predator scents resulting in greater climbing (Fig. 4b) and movement of the head and limbs, than a negative control. Geckos from Turakirae Head licked their snouts more often in response to rat cues, and those from Pukerua Bay licked less often in response to tuatara cues.

Site-specific differences in gecko activity were driven primarily by differences between sites with introduced mammals present when compared with mammal-free sites. Geckos from sites in which mammals were present (Pukerua Bay and Turakirae Head) spent more time walking (Fig. 4c) and running, and snout-licked more frequently (Fig. 4d), than those from sites where mammals were absent. Geckos from Pukerua Bay spent less time nudging the enclosure wall than geckos from other sites.

5.4.3 Does coevolution with mammalian predators influence lizard behaviours and predator detection abilities?

Introduced rainbow skinks, which co-evolved with mammals, differed from native common skinks in their behavioural responses to scent stimuli ($F_{16,372} = 2.952$, p < 0.001). Differences were attributable to rainbow skinks spending more time moving head, limbs and tail in response to both a novel scent (positive control) and rat chemical cues ($t_{194} = 2.512$, p = 0.013 and $t_{194} = 2.847$, p = 0.005, respectively) and elevating tongue flicking in response to a novel scent to a greater extent ($t_{194} = 3.264$, p = 0.001) than common skinks. Additionally, rainbow skinks were more active than common



Figure 4. Behavioural actions of common geckos, *Hoplodactylus maculatus*, in response to scent stimuli (a & b), and in relation to sites from which geckos were sourced (c & d). Behavioural actions portrayed are time spent: (a) running, (b) climbing, and (c) walking, and (d) number of snout licks. Site abbreviations are: 'NBI' = North Brother Island, 'SI' = Stephens Island, 'PB' = Pukerua Bay, and 'TH' = Turakirae Head.



Figure 5. Behavioural variation among native common skinks, *Oligosoma nigriplantare polychroma* (Onp) and introduced rainbow skinks, *Lampropholis delicata* (Ld) according to history of evolution with introduced mammalian predators. Rainbow skinks co-evolved with mammals (Y), while some common skink populations do not co-exist with mammals (N; either over evolutionary time, or now), and others have recently (R; within the last 1800 y) been exposed to mammalian predators. Behaviours shown are time spent: (a) slow walking, (b) nudging the enclosure wall, and (c) motionless, as well as (d) number of tongue flicks during the trial.

skinks across a range of activities in trials, and their lingual sampling of the substrate was more frequent (Table 2; Fig. 5).

5.5 Discussion

5.5.1 Chemoreceptive abilities of New Zealand lizards

I find little evidence to suggest that New Zealand lizards use chemoreception to detect and respond to predators, either native or introduced, regardless of whether they are abundant or rare in the presence of introduced mammals. Skinks do not appear to differentiate at all between scent stimuli presented, while geckos show some scent recognition, but respond to a novel cue at least as much as they do to predator chemical cues. The only indication that geckos may respond differentially to predator scent was an increase in running escape behaviour in response to rat chemical cues. However, as running activity among geckos was negligible and not accompanied by an increased frequency of lingual sampling, the correlation is unlikely to be biologically meaningful.

The finding that chemical cues induce native New Zealand geckos to modify behaviours to a greater extent than sympatric skinks runs contrary to predictions based on phylogenetically constrained chemical discrimination abilities (Cooper 1995a) and time of isolation from mammalian and snake predators (80 my for geckos and 10-25 my for skinks; Daugherty *et al.* 1990b, Hickson *et al.* 2000, Chambers *et al.* 2001). However, as skinks showed greater vomerolfactory sampling (Fig. 2) and behavioural responses of New Zealand geckos did not seem to be specific to predator chemical cues, this finding must be treated with caution.

Chemical cues of a native, ground-dwelling reptile (tuatara) did not elicit a specific antipredator response in sympatric native gecko or skink populations, with which they coevolved. In contrast, skinks and geckos elsewhere often show strong

aversion to chemical cues of reptilian predators. For example, Australian skinks, *Eulamprus heatwolei*, avoid predatory snakes and invertebrates (Head *et al.* 2002) and geckos, *Oedura lesueurii*, show antipredator responses to snake predators (Downes & Shine 1998, Downes & Adams 2001). My finding provides support for the hypothesis that chemosensory mediated antipredator behaviours are not well developed in New Zealand lizards, which have experienced relaxed selection pressure on this trait.

Chemoreception does not appear to mediate detection or avoidance of mammalian predators of lizards, irrespective of coevolution or experience of this predatory threat. Despite prey avoidance of predator chemical cues being demonstrated across a wide range of taxa (Kats & Dill 1998), the role of chemoreception in the detection and avoidance of mammalian predators by reptiles has received little attention (Kats & Dill 1998). However, novel defensive postures by rattlesnakes, *Crotalus cerastes* and *C. viridis oreganus*, in response to chemical cues of skunks, *Spilogale phenax phenax* (Cowles 1938), indicate that chemoreception is used by some reptiles to avoid mammalian predators. Furthermore, several sit-and-wait predatory snakes show a chemosensory ability to detect mammalian prey. For example, timber rattlesnakes, *Crotalus horridus*, show elevated tongue flicking rates and a greater tendency to adopt ambush postures to chemical cues from a range of mammalian prey including ship rats (Clark 2004) and rodent saliva elicits higher tongue flicking rates and tendency to strike in both brown tree snakes, *Boiga irregularis*, and prairie rattlesnakes, *C. viridis* (Chiszar *et al.* 1997).

Two main reasons for the differences in snake and lizard antipredator responses to mammalian scent exist: (1) chemosensory abilities of snakes are more highly developed than those of other squamate reptiles, and evolution of chemoreception is conservative (e.g., Schwenk 1995), and (2) chemosensory detection of widely foraging predators may not accurately reflect predation risk (Head *et al.* 2002), particularly during the active

phase of the predator. Understanding of the extent of chemosensory detection of mammalian predators by reptiles would be enhanced by using snakes as well as lizards as focal prey species (discussed in Chapter 6).

5.5.2 Behavioural patterns of lizards living in sympatry vs. allopatry with introduced mammals

Although not mediated by chemoreception, behavioural patterns of New Zealand lizards are highly correlated with the predator regimes to which they are exposed. Recent coexistence with predatory mammals seems to have induced a shift from antipredator freeze behaviour towards greater activity among lizards. The trend was exemplified by a behavioural comparison between common and rainbow skinks, the latter of which coevolved with mammalian predators (Fig. 5).

Behavioural differences between wild populations of native Duvaucel's geckos that are sympatric with introduced rats and those under a natural predation regime (Chapter 3) support this lab-based evidence. My findings suggest that when predatory mammals are introduced into a system formerly dominated by avian predators, they induce a shift from primarily visual antipredator strategies (freeze behaviours and crypsis) that enable avoiding detection (e.g., Appendix 1) to one in which escape behaviours also play an important role.

Similar behavioural shifts are induced by introduced predators in a range of prey species and may indicate adaption of some prey species to novel selective pressures (reviewed by Strauss *et al.* 2006). For example, predatory cats, *Felis catus*, induce greater wariness among lava lizards, *Tropidurus* spp, in the Galápagos archipelago (Stone *et al.* 1994). Variation in antipredator responses, and the ability to behaviourally adapt to novel selective pressures, enable some evolutionarily naïve prey species to coexist with exotic predators (Stone *et al.* 1994, Bunin & Jamieson 1996). However,

such adaptations may ultimately lead to the loss of behavioural diversity and altered

evolutionary trajectories.

CHAPTER 6

Community, population and individual level influences of introduced mammalian predators on native lizard prey

> Research synthesis, conservation implications and future directions

6.1 Effects of introduced mammalian predators on evolutionarily naïve lizard prey: a research synthesis

Evolutionary and behavioural changes in native species in response to selection from exotics are often overlooked, yet common responses include altered antipredator behaviours, changes in habitat use, altered growth and life history patterns, and morphological adaptations (Losos *et al.* 2004, Phillips & Shine 2004, Schoener *et al.* 2005, Phillips & Shine 2006, Strauss *et al.* 2006). Such adaptations often allow native populations to persist in invaded areas, while failure to adapt can lead to local extinction. Comparative frameworks using time-series comparisons or comparisons of native populations in invaded and uninvaded areas provide strong correlative evidence of adaptive responses induced in natives by invaders (Strauss *et al.* 2006). Furthermore, removal of invaders is a logistically difficult and seldom-used yet powerful technique for elucidating evolutionary and behavioural patterns in native species driven by invaders (Towns 1996, 2002a, Strauss *et al.* 2006). Biogeographic patterns in endemic New Zealand lizards (Daugherty *et al.* 1993, Towns & Daugherty 1994) and current conservation practices involving eradication of mammals from islands (Towns & Broome 2003) provide comparative and experimental frameworks in which to explore the mechanisms enabling persistence of some lizard populations now sympatric with introduced mammals.

In this dissertation, I explore the relationship between invasive mammalian predators and their endemic lizard prey in New Zealand at community, population and individual levels. My goal is to investigate how lizards are affected by mammalian predators, how they may have adapted to mammalian predation pressure, and how they respond once this pressure has been released.

A long-term (1984-2006) dataset derived from monitoring of the Pukerua Bay (North Island) lizard guild, which includes the last known mainland population of the large, endemic New Zealand skink, Cyclodina whitakeri, provided an opportunity to test whether capture rates of endemic lizard populations exposed to synergistic effects of invasive mammalian predators and habitat changes are continuing to decline (Chapter 2). Cyclodina whitakeri (nocturnal) and sympatric C. aenea (crepuscular) declined over the 23 year period, with capture rates approaching zero in both species by 2006. In contrast, capture rates of the sympatric diurnal skinks, Oligosoma nigriplantare polychroma and O. zelandicum, remained stable, and nocturnal geckos Hoplodactylus maculatus increased in capture frequency during the same period. Introduced mammals continue to disproportionately affect ground-dwelling species with relatively large body sizes or a primarily nocturnal activity phase (Chapter 2), despite having coexisted with mammals for at least 1000 y (Anderson 1996). Species with a combination of these attributes are most vulnerable to mammalian predation (Chapter 2). At both Pukerua Bay (Chapter 2) and central Otago (Tocher 2006), where populations of high conservation importance remain exposed to mammalian predators, the most vulnerable mainland populations are continuing to decline despite conservation efforts.

In contrast, lizards represent a numerically and ecologically important component of island ecosystems that have either remained free of introduced mammals or from which introduced mammals have been eradicated (Towns & Robb 1986, Keall et al. 2001). Examining the biogeography of endemic lizards has led to an understanding of the population-level impacts of introduced mammals (Towns & Daugherty 1994). My research adds to the limited body of research on the behavioural and ecological modifications that enable native species to persist in the presence of introduced mammals. A study of the population structure, behaviour and microhabitat use of Duvaucel's geckos, H. duvaucelii, and kiore, Rattus exulans, on three New Zealand offshore islands with different histories of rat invasions and eradication (Chapter 3) demonstrated that although kiore and Duvaucel's geckos share habitat at a broad spatial scale, little overlap in micro-habitat use exists in sympatry. In the presence of rats, Duvaucel's gecko capture rates and recruitment were low. However, six months after rat eradication and prior to any recruitment, capture rates of adult geckos increased fourfold, and geckos were using a greater proportion of habitat preferred by rats. Spatial avoidance of introduced rats by native geckos appears to be a highly plastic response to rat presence sometimes enabling their persistence in sympatry with rats. The same behavioural mechanism may facilitate survival of native prey species in sympatry with mammals on the New Zealand mainland (Chapter 2). However, the sensory mechanisms by which some New Zealand lizards are able to detect and spatially avoid introduced mammalian predators are poorly understood (but see Chapters 4 & 5).

Animal life history strategies evolve in response to a range of selective pressures and are often tightly linked to sensory cues. Squamate reptiles possess well developed chemosensory systems which evolved early in their history and remain highly conserved (Schwenk 1993, Cooper 1995a). However, the implications of isolation from mammalian predators for chemosensory antipredator abilities are unclear. The natural antipredator characteristics of New Zealand lizards involve avoiding detection by avian and reptilian predators through visual crypsis (Appendix 1); whether relaxation of chemosensory detection abilities accompanies a primarily visual antipredator strategy is unknown. I investigated (1) the ability of lizards under a natural predation regime to use chemoreception to detect and behaviourally respond to food, conspecifics, and native reptilian predators (Chapter 4), (2) potential correlations between chemosensory ability of New Zealand lizards to detect predators (both native and introduced) and their exposure to predators (Chapter 5), and (3) interspecific variation in ability of native lizards to detect and respond to predator chemical cues as a mechanism for vulnerability to mammalian predation (Chapter 5).

Chemosensory cues mediated gecko interactions with food and conspecifics, although I find little evidence of specific antipredator responses being elicited by predator chemical cues (Chapters 4 & 5). Skink behaviours did not vary according to chemical cues presented, and I found no differences in the chemosensory ability of rare versus common lizards to detect predator chemical cues (Chapter 5). However, behaviours of native lizards were correlated with the presence of introduced mammals. Lizards recently exposed to mammalian predators were more active and spent less time in antipredator freeze postures than those remaining in isolation from mammals; this laboratory-derived evidence supports conclusions from the field that introduced mammals induce behavioural shifts in native lizard populations (Chapter 3).

In relation to the hypotheses set up in the introduction of this dissertation (Chapter 1) I found that:

 Not all lizard populations that have persisted on New Zealand's mainland have reached an equilibrium with introduced mammalian predators; instead large, nocturnal and terrestrial species remain highly vulnerable (Chapter 2). Arboreal geckos exploit vertical habitat if rodents are present (Chapter 3), which gives insight into how some species can persist with mammals.

- 2. Introduced mammals can induce highly plastic behavioural shifts in native reptiles, which may facilitate spatial avoidance and hence reptile population persistence (Chapter 3).
- 3. Activity patterns of lizards are correlated with their coevolution and experience with mammalian predators; activity levels increase and antipredator freeze behaviour decreases with greater exposure to mammals (Chapter 5). Antipredator responses to mammals are not elicited by chemical cues alone (Chapter 5), even though some native lizards behaviourally respond to the scent of fruit and conspecifics (Chapter 4).

6.2 Conservation implications

Research into population trends of lizards at mainland sites, which are subjected to sustained mammalian predation pressure (Chapter 2), supports an emerging conclusion that current management practices directed at conserving threatened lizard taxa on mainland New Zealand are ineffective (Tocher 2006). Research seeking to identify agents of decline in mainland lizard populations is urgently needed so that effective management solutions can be implemented. However, dedicating time to locate the source of declines is no longer possible for a number of important threatened populations (Chapter 2). The species at most risk on the mainland are likely to continue to decline or disappear at mainland sites without immediate and intensive solutions. In the face of synergistic effects between habitat change and introduced species, the use of mammal exclosures may be the only option available to conserving rare and declining lizard populations on the mainland.

Conserving species and populations is less problematic if they either occur naturally on offshore islands or remain in sufficient numbers to source founders for translocation to a mammal-free offshore island with suitable habitat. Current mammal eradication techniques used in New Zealand ensure population recovery and security of many threatened lizard species, as well as securing habitat for native species reintroductions (Towns 2002a, Towns & Broome 2003). Evidence from populations released from mammalian predation pressure through eradication and those which have been reintroduced to mammal-free offshore islands demonstrates the effectiveness of this technique for conserving lizards (Towns 1996, 2002a, Towns *et al.* 2003). However, my research suggests that rodent eradication can restore not only populations, but also natural behaviours of individuals within those populations (Chapter 3). Lizard behavioural shifts and species rediscoveries following rodent eradication emphasise the need to allow a sufficient lag time to detect species before any restorative species reintroductions are considered (Chapter 3).

6.3 Future research directions

My work has generated a number of avenues for further research into the abilities of naïve prey to respond to novel predators with both theoretical and conservation implications. I specifically recommend research into the following:

 How invasive plant and animal species interact to exacerbate declines of vulnerable mainland lizard populations. Many of the endemic New Zealand lizards that were widespread throughout the mainland are now restricted to offshore islands. Some of those that have persisted in the presence of a range of mammals continue to decline to the point of extinction, despite management efforts (Chapter 2; Tocher 2006). Experimental manipulations using new fencing technology to exclude mammals and simultaneous pest plant control would provide a test of the individual and synergistic effects of invasive species on vulnerable lizard populations.

- 2. The prevalence and extent of adaptive behaviours of native prey species in response to introduction of novel predators. Native geckos modify their behaviours and use of habitat in the presence of introduced rodents and can therefore persist at undetectable levels (Chapter 3). Evidence of life historical, morphological and behavioural shifts induced by novel predators in other taxa suggests that rapid selection for such antipredator traits may be a mechanism by which novel prey survive with novel predators (McIntosh *et al.* 1994, Rufaut & Gibbs 2003, Strauss *et al.* 2006). Investigating patterns of these predator-induced shifts in a range of native taxa on New Zealand islands with different suites of introduced mammals would provide strong correlative evidence to test this hypothesis.
- 3. The ability of squamate reptiles that have coevolved with predatory mammals to detect and respond to them using chemical cues. Despite extensive literature searching, I found almost no research into chemosensory mediated antipredator behaviours of lizards exposed to mammalian chemical cues. The only exception is an intriguing account of novel defence postures elicited in rattlesnakes by skunk scent (Cowles 1938). Although mammals are often active foragers, chemical avoidance of mammal retreat sites would seem beneficial for reptiles. The one skink species that had coevolved with mammals and was used as an out-group in my chemosensory study responded similarly to novel scent and rat chemical cues (Chapter 5); this negative result neither supports nor disproves the hypothesis that antipredator responses of squamate reptiles are elicited by mammalian chemical cues. Testing the chemosensory abilities of a range of

reptiles that have coevolved with mammalian predators to detect mammals, using accepted methodology developed in snake predator-lizard prey systems (e.g., Downes & Shine 1998), would enhance understanding of these predatorprey relationships.

- 4. Loss of antipredator responses to snake scent in introduced skinks. Biological invaders, which often thrive in the absence of coevolved predators, provide an opportunity to test hypotheses about the evolution of predator-prey relationships (e.g., Chapter 5). Rainbow skinks, *Lampropholis delicata*, which have invaded New Zealand, Hawai'i and Lord Howe Islands (Baker 1979, Gill & Whitaker 1996, Peace 2004, Hutchinson *et al.* 2005) over the past century provide an outgroup with which to compare chemosensory detection abilities of native species (Chapter 5), but could also be used to test loss of antipredator behaviours during the course of relaxed selection. Rainbow skinks show chemosensory-based avoidance of predatory snakes in their native range (Downes & Hoefer 2004), but have been isolated from these predators for 10 100 years (Baker 1979, Hutchinson *et al.* 2005) in their exotic range. This natural experimental system could be used to assess relaxed selection.
- 5. The chemical conspicuousness of native prey that have evolved in isolation from mammals as a trait that increases their vulnerability to mammalian predation. Chemosensory interactions between novel predators and naïve prey remain poorly understood. Isolation from mammalian predators that hunt primarily by scent may have led to relaxed predator detection abilities (Chapter 5). However, in isolation from mammals, prey may also develop their use of odour for conspecific communication (Chapter 4; Worthy & Holdaway 2002). In this case, prey may become particularly conspicuous to introduced predators hunting by scent (Worthy & Holdaway 2002). I recommend testing: (1) the use of

chemoreception by native (tuatara and bird) and introduced (rodent and mustelid) predators of New Zealand lizards in prey location, and (2) the chemical conspicuousness of New Zealand lizards relative to lizards that evolved with mammalian predators.

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APPENDIX 1

Investigating natural population dynamics of *Naultinus manukanus* to inform conservation management of New Zealand's cryptic diurnal geckos¹

Abstract

Visually cryptic, long-lived, diurnal green geckos (genus *Naultinus*) were a significant component of natural ecosystems throughout much of New Zealand prior to human settlement 1800ya. Since then, habitat modification and introduced mammalian predators have threatened many *Naultinus* populations, making their survival a conservation priority. However, the visually and behaviourally cryptic nature of *Naultinus* geckos and a lack of scientific attention pose challenges to their conservation management. We investigate natural population dynamics of the Marlborough green gecko (*Naultinus manukanus*), to act as a model for understanding the ecology of New Zealand's diurnal geckos and to inform conservation management. The largest known *N. manukanus* population (on mammal-free Stephens Island) has been the focus of several studies along a bush-edge transect. We pooled data obtained using mark-recapture, population census, captive rearing of juveniles and radio telemetric methodologies over 25 y to examine aspects of their ecology and behaviour. The population is female-biased (1:1.7 M:F), a trend that is apparent from birth, and exhibits

¹ **Based on:** Hare, K.M., J.M. Hoare and R.A. Hitchmough. Investigating natural population dynamics of *Naultinus manukanus* to inform conservation management of New Zealand's cryptic diurnal geckos *Journal of Herpetology* (accepted). My contributions were the radio-telemetric study and morphometric information from geckos caught in November 2004 (Chapter 5).

sexual size dimorphism, with adult females larger than males. Sexual maturity occurs at approximately 4 y of age and 71% of females reproduce annually. *Naultinus manukanus* are strictly diurnal, arboreal and opportunistic thermoregulators. Daily movements are very limited, averaging 0.6 m per day, characteristic of the sit-and-wait foraging strategy that they employ. The basic ecological information presented in this paper provides context for the conservation management of *Naultinus* species, which are increasingly recognised as threatened in their current ranges.

Introduction

Human settlement has had major impacts on New Zealand's terrestrial vertebrate populations through habitat loss and introduction of mammalian predators. For reptiles alone, approximately one third are now restricted to mammal-free offshore islands (Towns & Daugherty 1994). Within the lizards, three species have become extinct, and many others show disjunct or dramatically reduced ranges (Towns & Daugherty 1994). Currently, over 80 species of lizard (including undescribed species) are present in New Zealand (Hitchmough *et al.* in press), but most lack descriptive studies of their basic biological information. Accurate biological information is important for conservation management, particularly to provide context and baseline data for current conservation management methods in New Zealand, post-translocation surveys and estimating population recovery times after predator removal (Bannock *et al.* 1999, Towns & Ferreira 2001).

The genus *Naultinus* is one of only two diurnal gecko genera within the family Diplodactylidae and contains eight described species endemic to New Zealand (Pianka & Vitt 2003, Han *et al.* 2004, Hitchmough *et al.* in press). Despite taxonomic studies of *Naultinus* geckos (e.g., Pringle 1998) and various incidental studies within larger research projects (e.g., Walls 1983, Bauer & Russell 1994, Cree 1994), few published studies specifically examine their reproductive biology, ecology and behaviour (but see Hitchmough 1982, Wilson & Cree 2003). As *Naultinus* geckos are very difficult to detect, especially at low densities (Whitaker & Gaze 1999), studies of large populations are useful for predicting management outcomes for threatened, low density populations.

The Marlborough green gecko *Naultinus manukanus* (McCann 1955) is a diurnal, arboreal, viviparous, cryptically-coloured gecko restricted to the Marlborough Sounds region of New Zealand. While populations are not known to be currently declining, *N. manukanus* is listed in the New Zealand threat classification system as 'sparse' (Hitchmough 2002). The largest known population is located on Stephens Island (Whitaker 1971, Hitchmough 1978, Whitaker & Gaze 1999). Habitat fragmentation, continuing loss of seral shrub-land habitat, a full suite of introduced mammalian predators through most of its range and food competition from introduced vespulid wasps all provide potential threats to the survival of *N. manukanus* on the mainland (Whitaker & Gaze 1999).

Efforts to define the distribution of *Naultinus* species have been hampered by detection difficulties due to their secretive habits and cryptic colouration (e.g., Whitaker 1994, Whitaker & Gaze 1999). Knowledge of microhabitat use, including habitat preferences, movement patterns and use of retreat sites, provides ecological information helpful in locating cryptic species (e.g., Neilson *et al.* 2004). Thus, study of preferred habitat and movement patterns will contribute to defining likely habitats to search, and hence successful conservation management (Whitaker & Gaze 1999). We estimated habitat use, baseline data on population structure, and morphometrics of *N. manukanus*, to aid conservation management and identify potential problems for population viability.

Methods

Stephens Island (Takapourewa; 40°35'S 173°55'E) is a 150 ha Nature Reserve located at the northern tip of the Marlborough Sounds, Cook Strait, New Zealand, and is the site of a number of long-term ecological studies (e.g., Brown 1994, Nelson et al. 2004, Hare & Cree 2005). The advantages of collecting long-term rather than shortterm data are well known (e.g., Tinkle 1979, Gibbons 1987, Madsen & Shine 2001, Hoare *et al.* in press). However, the logistical difficulties of conducting long-term studies mean that they are rare (Madsen & Shine 2001). We provide data from five studies of *N. manukanus* on Stephens Island collected over 25 y along the same stretch of habitat, a ridge-top bush edge transect, that spanned 300 m in 1978 and 440 m in later studies (due to regeneration; effective searching within 1.5 m of each side of the track). The slopes of Stephens Island between the cliffs and summit were once covered by dense native forest (Dieffenbach 1843). However, lighthouse operations and associated activity since 1892, as well as World War II battlements, led to the loss of approximately 90% of the original forest (Walls 1983, Brown 2000). Since 1987 intensive revegetation efforts have replaced pasture grass areas with small shrubs and regenerating forest (Brown 1992). From 1990 to 2002 alone the vegetation cover has increased from 5.5 ha to 21.6 ha (Hare & Cree 2005).

The first of the five studies was a population survey in January 1978 (Hitchmough 1978). The second included collection of 30 adults for metabolic experiments (Hare 2005). The third was a wild population count in March 2003, where 30 adults were captured for translocation to Whakaterepapanui Island. The fourth study included collection of 30 individuals in November 2003 for a behavioural study (Chapter 5). The final study employed radio telemetry in November 2004 to investigate microhabitat use of these geckos. The combination of data from these five studies is appropriate as each

provides information on a different part of their ecology and, where the same methods were used, the data can be pooled for analysis. These studies enable us to provide comprehensive information on the ecology and behaviour of the largest known wild population of *Naultinus manukanus*, and an insight of the ecology of one of New Zealand's visually cryptic diurnal geckos.

Data collection

January 1978 mark-recapture study: The vegetation along the bush-edge transect was searched from 5 to 17 January 1978 and geckos captured by hand. At first capture each animal was weighed (to 0.5 g) and its snout-vent length (SVL) and venttail length (VTL) measured (± 0.1 mm). All animals had a description made of skin colour and any mite infestation, as well as sex and the reproductive status of all females, including pregnancy status (yes/no) and number of embryos felt by abdominal palpation (see Cree & Guillette 1995 and Wilson & Cree 2003 for accuracy of this procedure in other New Zealand geckos). Each animal was numbered on both flanks with a black felt-tipped pen, and a numbered tag attached to the twig on which it was first seen. When located subsequently the animal was identified by its number and the distance from the initial capture point estimated. At each capture or recapture, the date, time, weather conditions (presence or absence of sunshine, temperature, estimates of wind strength and cloud cover) and vegetation species on which geckos were found were noted.

March 2003 count and animal collection: The vegetation along the bush-edge transect was searched and geckos captured by hand. Thirty adult *N. manukanus* (10 males, 10 non-pregnant females and 10 pregnant females) were collected from 9 to 14 March 2003, for translocation to Whakaterepapanui Island. All captured animals had vegetation type, toe or tail loss status (yes/no) and sex recorded. Reproductive status of

all females was also recorded, including pregnancy status (yes/no) and number of embryos felt by abdominal palpation. Geckos were 'screened' in the field as to their suitability for translocation, and only animals chosen (adult, required sex ratio and reproductive status) for translocation had morphological measures and characteristics recorded, including mass (\pm 0.1 g), SVL, VTL (\pm 0.5 mm), skin colouration and number of mites. Animals not included in the translocation were included in the count census, semi-permanently marked on the ventral surface and immediately released at the point of capture without metric measurements taken to limit stress of handling. Three extra females were also measured, but not included in the translocation.

November 2002 and 2003: Both studies in November 2002 and 2003 were conducted to provide animals for physiological and behavioural experiments (e.g., Hare 2005, Hare *et al.* 2006; Chapter 5). The vegetation along the bush-edge transect was searched during daylight hours and geckos captured by hand. Only those animals taken for experiments had parasite load, morphometric measurements (SVL, VTL and mass), and vegetation type recorded. No other data were collected at this time to limit disturbance to non-experimental animals.

November 2004 radio telemetry study: Five adult geckos (two males and three females) were captured from 1 to 6 November 2004 for a microhabitat study. The geckos were from a 1438 m² area of regenerating forest which overlapped the bush-edge transect along the northern 130 m. All five geckos had mass \geq 9.75 g and were fitted with small (ca. 1 g) radio transmitters (Sirtrack[®], Havelock North, New Zealand, < 10% of body weight) using a 'backpack' method of attachment which has proven effective in other New Zealand geckos (Schneyer 2001, Salmon 2002). The five geckos were located hourly during the day between 6 am and 6 pm inclusive (in a preliminary study of one gecko over two nights there were no movements between 6 pm and 6 am).

All geckos within the main telemetry study were within 0.2 m of their 6 pm location at 6 am the following morning.

Geckos were tracked over five to eight days (in a single period) to assess microhabitat use, daily movement patterns and selection of nocturnal retreat sites. At each location, gecko positions found by telemetry and vegetation characteristics were measured. These included plant species on which the gecko was found, its height above ground, part of vegetation used (e.g., foliage, stem, branch, trunk, ground), whether the gecko was sighted (yes/no), its distance from the surface of the vegetation, direction and distance from previous position and any behavioural observations.

We recorded the height, radius (including foliage) and area occupied by each plant species within a 5 m circle of the point of capture of each gecko to obtain a measure of habitat availability. No gecko moved further than a straight line distance of 5 m during the study. Mean and maximum daily air temperatures, wind speed, humidity, rainfall (in the previous 24 h) and cloud cover were also recorded. Weather information, other than temperature data, was obtained from the New Zealand MetService weather station on the island. Ambient temperature was recorded in the shade at 1.3 m above ground in the centre of the telemetry area, and local temperature data were recorded for each gecko at the point of capture, using waterproof Stowaway[®] TidbiT[®] temperature recorders (Onset Computer Corporation, Massachusetts).

Juveniles born in the laboratory: The 10 pregnant females housed at Victoria University of Wellington (VUW) prior to translocation to Whakaterepapanui Island gave birth in captivity (see Hare *et al.* 2004 for husbandry descriptions of captive-held adults). Juveniles were kept in similar conditions to adults. The females were weighed and measured within 12 h of parturition. Following birth, juveniles were semipermanently marked with a unique number using a black marker, weighed to 1 mg (on a Sartørius top loading balance), and SVL and VTL were measured to 0.5 mm. Juveniles were again measured at 1, 2, 4, 5 and 6 months of age. The ventral surface of juveniles was inspected at each monthly measuring to determine whether sex was apparent by ventral colouration (white in males and pale green in females). Juveniles were permanently marked by toe-clip on either their fourth or fifth monthly measure prior to release. Juveniles were housed in their birth groups (two individuals), and in one case (where a juvenile had no siblings) in a group of three.

Data analyses

Data were analysed using the statistical programme *R* (Ihaka & Gentlemen 1996; Version 1.9.1). All data were tested for normality, and statistical significance was assumed at *P* < 0.05. Data are expressed as mean \pm 1 SE unless otherwise stated.

Natural population dynamics: We compare data only from January 1978 and March 2003 for the natural population dynamics, as these data include physical descriptions of all individuals seen and captured in the population, as well as morphometric measurements (SVL, VTL and mass) of all adults in 1978 (N = 22) and a large sample of selected adults (71% of all adults captured) in March 2003 (N = 33individuals, including three females not translocated). For all individuals in the population we provide information on capture rate (geckos/person hour), population density, sex ratio, frequency of tail loss and colour markings. Body condition (BC) was calculated using the residuals from fitted data using a linear regression of log mass on log SVL.

Prior to adult morphometric analyses of combined 1978 and March 2003 data, we compared all size data from 1978 with those of March 2003 to ensure there were no differences over the 25 y period. As all *P* values exceeded 0.05 we pooled all morphometric data for further analyses. We analysed whether size is sexually dimorphic in *N. manukanus* by assessing the differences in SVL, mass and body

condition (BC) between all adult males and females (pregnant and non-pregnant) using a general linear model (GLM) with sex (including pregnancy status) as the independent factor and SVL the dependent variable. We also tested whether length of tails (complete tails only) varied with sex and pregnancy status by using a GLM with sex (including pregnancy status) as the independent variable, VTL as the dependent variable and SVL as a covariate accounting for overall animal size. We analysed whether tail loss as an adult (status = yes/no) differed between males and females using Chi-squared (χ^2) analyses.

The mark-recapture programme Mark (White 2005) was used to calculate a population estimate from 1978. A closed population model was used, and three models were implemented: a single capture probability model (no variance: null), a temporal model (to assess variance over time) and a behavioural model (to assess capture happiness/shyness of animals). Akaike's Information Criteria (AIC; Akaike 1978, Burnham & Anderson 1998) were used to select the model(s) that best explained the data, and values were then rescaled to the lowest AIC to give relative AIC values (Δ AIC). Those models with the lowest AIC values provide the best explanation of variance (Burnham & Anderson 1998). Where two alternative models have an AIC difference of < 2, both were included. The *F* statistic measures the overall value of the predictors and compares the chosen model with the null model.

Seasonal differences: We compared data from adult individuals captured in January 1978 (N = 22; summer), November 2002 (N = 30; spring), March 2003 (N = 33; late summer/early autumn) and November 2003 (N = 17; spring) to determine whether BC and mite numbers differ seasonally. Models were developed with trip, number of mites, tail loss, sex and pregnancy status (and their various interactions) included as dependent fixed effects and individual as an independent random variable. The models were compared using AIC analyses. Habitat use and movement patterns: Comparing available habitat with gecko positions, located using radio-telemetry, we calculated macro- and micro-habitat use as well as documenting nocturnal locations. Habitat use was calculated by comparing available habitat with what the geckos used during the study period with χ^2 tests. Vertical use of vegetation was also investigated, relative to the height of vegetation available using χ^2 tests, categorizing vegetation height as 'low' (< 0.3 m), 'medium' (0.3 to < 1.5 m) or 'high' (\geq 1.5 m) to represent major vegetation types (grass matrix, shrubs and trees respectively).

Factors governing the daily movement of *N. manukanus* were investigated using daily recorded movements and height above ground as dependent variables in a multivariate analysis of variance (MANOVA). Individual variation was allowed for by including individual as an independent random factor in analyses. Gecko movement data on the day of capture were excluded from analyses to exclude potential behavioural changes immediately after transmitter attachment, as human contact is known to influence lizard behaviour (e.g., Kerr *et al.* 2004). Additionally, the day since capture was included as an independent factor in analyses to assess potential influences of capture on movement patterns. Mean and maximum daily ambient air temperatures, wind speed, humidity, rainfall (in the previous 24 h) and cloud cover for Stephens Island were included in analyses as fixed factors to assess their potential influence on gecko movements. Use of habitat during the inactive period at night is described in relation to habitat availability.

Movement patterns, irrespective of height of the gecko above ground, were investigated in more detail using a univariate ANOVA with daily movements as the dependent variable, and tracking day and the climatic variables as fixed factors, though this model did not account for individual variation. Potential influences of temperature on hourly gecko movements were investigated using an ANOVA with movements as the dependent variable and local temperature for each gecko as a fixed factor.

Juvenile morphometrics: Overall size at birth and 6 months was assessed using a GLM with independent factors of sex, maternal SVL or maternal BC, dependent factors of all juvenile size measures separately and individual as a random factor. Growth rate (mm/day) was based on the difference between SVL at birth and at 6 months of age using a linear model, with sex as the independent factor, and SVL at birth as a covariate. Analyses containing the above factors as well as maternal SVL, maternal BC postpartum, and BC of juveniles at birth were also compared.

Results

Natural population traits

In January 1978 the capture rate of *N. manukanus* was not estimated, but 29 individuals were seen and captured. Population size for the area searched was estimated as 41 ± 6 geckos (95% confidence interval = 32 to 64 geckos), which translates to an average density of 0.05 geckos/m². The single capture probability model best explained the data. In March 2003 the capture rate was 3.37 geckos/person hour along the ridge track; 69 animals were seen and 65 were captured. The population density in 2003 was also 0.05 geckos/m² (N = 43) along both the same 300 m searched in 1978, and the regenerated 140 m section. Recruitment into the population was evident in both years by the capture of pregnant females (N = 10 in 1978; N = 24 in 2003) and the presence of juveniles and sub-adults (N = 7 in 1978; N = 14 in 2003).

Most captures were made during daylight hours in both January 1978 and March 2003 (100% in 1978 and 88% in 2003). Eight individuals were opportunistically captured at night during the 2003 survey while searching for the arboreal nocturnal

gecko *Hoplodactylus stephensi* (Hare & Cree 2005). No individuals had characteristic markings in 1978, with all adults and juveniles a uniform green on the dorsum. In 2003, 20% of the population had dark blue colour markings of no larger than 1 mm in diameter on the dorsal surface; spots were located at random positions from head to tail tip.

The sex ratio of captured animals (including sub-adults) was 1:1.9 M:F in 1978 and 1:1.7 M:F in 2003. Of the 14 adult females captured in 1978, 10 (71%) were pregnant, and the reproductive output of the population was 1.28 offspring/female/year (Hitchmough 1978, Cree 1994). Of the 34 adult females captured in autumn 2003, 24 (71%) were pregnant with either one embryo (8%) or two embryos (92%) identified by palpation, equating to an annual reproductive output of 1.35 offspring/female/year.

The frequency of tail loss for this species was 14% of the sampled adult population in 1978 and 10% of the sampled adult population in 2003 with no difference between males and females (adults) in tail loss for either year ($\chi^2_1 = 0.001$ and 0.176 respectively). All sub-adults had complete tails and were therefore not included in tail loss analyses. In 2003 10 individuals (15%) had natural toe loss, no more than one toe was lost from any individual. No data on toe-loss were collected in 1978.

Mature geckos (by secondary sexual characteristics) ranged in size from 64 to 81 mm SVL, 70 to 96 mm VTL and 3.0 to 12.5 g in mass (Table 1; Fig. 1). From size frequency data, it appears that maturity occurs at ca. 4 years of age (Fig. 1). Adult females were, on average, 5 mm longer than males, with pregnant females 3 mm longer than non-pregnant females, and non-pregnant females 2 mm longer than males ($F_{2,51}$ = 14.08, *P* < 0.01). Taking overall size of the individuals into account, and using data from individuals with complete tails only, pregnant females had tails, on average, 5 mm longer than non-pregnant females and males (*F*_{2,46} = 8.472, *P* < 0.01). Non-pregnant females or males (*F*_{2,46} = 8.472, *P* < 0.01). Non-pregnant females and males did not have significantly different tail lengths (*t*₁ = 0.102, *P* =

Table 1. Pooled morphological measurements of *N. manukanus* from Stephens Island for January 1978 (N = 22) and March 2003 (N = 33). Prior to pooling data statistical analyses were undertaken to determine whether there were significant differences in size measures over the 25 y time scale (all values > 0.05). All measurements are ± 1 SE. p = pregnant; np = not pregnant; SVL = snout-vent length; VTL = vent-tail length of complete tails only, subsequently [†]N = 16; [‡]N = 20; [§]N = 13; ^{††}N = 33; ^{‡‡}N = 49.

Sex			SVL (mm)		VTL (1	mm)	Mass (g)	
		N	Mean	Range	Mean	Range	Mean	Range
Male		17	68.9 ± 0.9	64 - 75	[†] 83.6 ± 2.0	71-96	6.8 ± 0.4	3.0 - 9.0
	р	23	74.6 ± 0.6	69 - 81	$^{\ddagger}87.8 \pm 0.7$	82 - 94	8.4 ± 0.5	5.0 - 12.5
Female	np	14	71.4 ± 1.1	65 - 81	82.3 ± 1.4	70 - 89	8.4 ± 0.5	5.8 - 11.0
	p + np	37	73.4 ± 0.6	65 - 81	$^{\dagger\dagger}85.6\pm0.8$	70 - 94	8.4 ± 0.5	5.0 - 12.5
Male + female		54	71.9 ± 0.6	64 - 81	^{‡‡} 84.9 ± 0.9	70 - 96	7.9 ± 0.3	3.0 - 12.5



Figure 1. Size frequency distribution of *Naultinus manukanus* from Stephens Island. Individuals above the horizontal line are females and below are males. Data are combined for captures in January 1978 and March 2003, and size at birth for juveniles born in the laboratory from 10 females captured in March 2003. Sub-adults span at least three cohorts and adults are 4+ years. [†]Neonates were born in captivity and indicate size range at birth.

0.919). Pregnant females and non-pregnant females did not differ in mass ($F_{1,31} = 0.029$, P = 0.864), but males had mass ca. 1.5 g lower than females ($F_{2,51} = 3.993$, P = 0.245). Variation in BC was related to individual variation (Δ AIC < 2), but not to any other measure tested.

Seasonal differences in body condition and mite load

The variation in BC among individuals within a trip was greatest in January 1978 and least in November 2002, but BC did not differ among trips. Variation in BC was explained more by individual variation than any of the other factors tested, including trip, sex, pregnancy status, tail regeneration, number of mites, or any interaction of these variables ($\Delta AIC > 4$ for all other variables; Burnham & Anderson 1998). The number of mites (probably *Neotrombicula naultini*, Goff *et al.* 1987) found on any individual was between 0 and 5. The low numbers of individuals with mites did not allow for statistical comparisons among seasons, but there was an apparent trend over the seasons. No individuals had mites in spring (November 2002 and 2003), two individuals had mites in summer (January 1978) and 6 individuals had mites in late summer/early autumn (March 2003).

Capture locations

The plant species that *N. manukanus* were located on differed through time. In January 1978 geckos were found on eight plant species, with 66% of individuals located on *Coprosma repens* or vines associated with *C. repens*. In November 2002 geckos were found on seven pant species, with the major plant species including *Ozothamnus leptophyllus* (50%), *Muehlenbeckia complexa* (20%) and *Melicytus* aff. *obovatus* (13%). In March 2003 geckos were found on 10 plant species, with the major plant species including *O. leptophyllus* (42%) and *Myoporum laetum* (15%). In November 2003 geckos were found on 11 plant species including 27% on *M. complexa*, 20% on *O. leptophyllus*, and 17% on *Tetragonia trigyna*. All plant species that geckos were located on (in the studies including the whole captured population; January 1978 and March 2003) are listed in Table 2. Geckos captured in November 2002 and 2003 were only located on plant species listed in Table 2.

Daily movement patterns

Naultinus manukanus do not move large distances over a period of hours or days. During the mark-recapture study in 1978 most individuals were re-sighted on the same bush as initial capture. Only one individual moved more than 3 m, a pregnant female which moved a straight-line distance of 10 m over eight days. No *N. manukanus* **Table 2.** Number of individuals of *Naultinus manukanus* located in different plant species along transect on the ridge top track on Stephens Island. All individuals in the population were captured for a mark-recapture study (January 1978; transect = 300 m) and a population census (March 2003; transect = 440 m).

Plant spacios	Ja	anuary 19	78	March 2003			
Fiant species	Male	Female	Total	Male	Female	Total	
Coprosma repens	5	10	15	1	0	1	
C. repens and Clematis paniculata	0	1	1	0	0	0	
C. repens and Calystegia sepium	2	1	3	0	0	0	
C. repens and Tetragonia trigyna	0	1	1	0	0	0	
Calystegia sepium	2	0	2	0	0	0	
Grass (sp. unknown)	0	0	0	1	1	2	
Ground (no vegetation)	1	1	2	0	0	0	
Muehlenbeckia complexa	0	0	0	0	3	3	
M. complexa x australis	0	0	0	1	3	4	
M. complexa and C. sepium	0	3	3	0	0	0	
Melicytus aff. obovatus	1	1	2	4	5	9	
Myoporum laetum	0	0	0	6	4	10	
Oleria solandri	0	0	0	2	2	4	
Ozothamnus leptophyllus	0	0	0	7	20	27	
Phormium cookianum	0	0	0	0	1	1	
Pittosporum tenuifolium	0	0	0	0	2	2	
Total	11	18	29	22	41	63	

were found on the surface of vegetation at ambient temperatures below 18 °C, and animals moved into shade when ambient temperatures reached 34.5 °C. Cloud cover did not reduce the number of animals sighted, unless associated with wind and/or reduced temperatures.

During the telemetry study in 2004, *N. manukanus* exhibited strictly diurnal movement patterns. Daily movement of the geckos was not influenced by time since capture ($t_{11} = 2.370$, P = 0.144), though movements on the day of transmitter attachment were excluded from analyses. Thus, we were able to exclude behavioural changes associated with transmitter attachment as a source of variation in movements. Gecko movements were very small, both on an hourly and daily basis. Over the five day period that individuals were radio-tracked the maximum total distance moved was 4.0 m. The average hourly movements of all individuals was 0.05 ± 0.01 m (range 0 to 2.06 m), while daily movements averaged 0.59 ± 0.10 m (range 0 to 2.35 m).

The 2004 radio-telemetry study demonstrated that geckos moved less on cloudy days than clear days ($t_{11} = -2.240$, P = 0.043), and were found up to 0.85 m beneath the edge of foliage on cloudy days. During the day, geckos were often found on the surface of the foliage basking in direct sunlight. Of all daytime sightings, 25.9% were on the canopy. If direct sunlight was not available, geckos moved beneath the canopy and into the vegetation, most often by 0.01 to 0.15 m (52.7 % of all observations), though they were found deeper than 0.15 m into the canopy 21.4 % of the time. Hourly movements of geckos were not significantly related to ambient temperature ($t_{257} = 1.410$, P = 0.160). Ambient temperatures during day hours ranged from 9.6 °C to 19.4 °C, though temperature in direct sunlight reached 31.0 °C. Geckos only moved at ambient temperatures above 12.4 °C.

Microhabitat use

Naultinus manukanus used the full structural range of habitat available, including the ground and trunks, branches, stems and leaves of coastal shrubs. Foliage was used the most (50.9 % of observations), followed by stems (23.6 %), the ground (18.7 %), branches (6.2 %) and trunks (0.6 %). Vertical use of vegetation was biased towards shrubs (0.3 to < 1.5 m height) and trees (\geq 1.5 m in height; $\chi^2_2 = 113.800$, *P* < 0.001). However, the ground was used as a means of reaching other shrubs and trees by two of the five geckos tracked. Geckos also used the full range of vertical habitat available, from the ground to 2.5 m above ground. Mean height of geckos above ground was 1.27 \pm 0.04 m, but this varied according to the vegetation available to each gecko.

Naultinus manukanus appear to use vegetation disproportionately to its availability $(\chi^2_9 = 941.500, P < 0.001;$ Fig. 2). Coastal shrubs over-used in relation to availability were *O. leptophyllus*, *O. paniculata*, *P. tenuifolium*, and *C. repens*. The only coastal tree species that appears to be under-used by *N. manukanus* in relation to its availability is *M. laetum*, although in March 2003 10 individuals were found on this vegetation. The matrix of mostly introduced grasses between coastal trees are also under-used and appear to represent habitat used in transit to other shrubs as opposed to selected habitat. Individual differences in habitat use were evident, and were related to habitat availability in the immediate vicinity of gecko captures. Individual movement patterns differed significantly ($F_4 = 11.690, P < 0.001$), and appear not to be related to sex.

Nocturnal locations

Thirty-two overnight positions used by the geckos (i.e., during their inactive period) were characterised (5 to 8 positions per individual). Geckos were never found in refugia such as subterranean locations or within tree holes, as sympatric nocturnal



Figure 2. Plant species used by five adult *Naultinus manukanus* within 247 m² over a 5 to 8 day continuous period in November 2004 in regenerating forest habitat. Proportion of habitat is calculated as proportion of vegetation available (in a circle of radius 5 m from each point of capture) subtracted from proportion of vegetation used (N = 416 observations). \blacksquare = proportion of time spent in habitat, \blacksquare = proportion of habitat available to geckos. 'Grass' is a matrix of native and introduced grasses (see Brown 2000 for species list).

Hoplodactylus geckos usually are during their inactive phase (J. Hoare, unpubl. data). Instead, nocturnal locations appeared to be the place at which the gecko stopped daily activity, usually when direct sunlight left the position in which the gecko was located. Most geckos retreated 0.05 to 0.15 m into the foliage at night (69.6 % of observations), though they were also found on the outside of the canopy (17.4 %) or well below the canopy (13.0 %; up to 0.85 m beneath canopy). Retreat sites used were anywhere between 0 to 2.0 m above ground and included sites amongst grass and on the stems and foliage of coastal shrubs and trees; Table 3). Geckos never returned to the same site as their previous night's location.

Juvenile morphology and growth

Juveniles were born between 25 March and 16 April 2004 (N = 19). All twins were born within 12 h of each other. All had uniform green dorsal and ventral surfaces at birth, except one that had three white spots on the dorsal tail base. The colour of the ventral surface changed with time, and sex of juveniles could be determined easily at two months of age by sexually dimorphic ventral colouration. Males have a white ventral surface and females a green ventral surface. The same dimorphic colouration is also apparent in adults. All but one juvenile survived to six months of age. The juvenile that died never appeared to eat (K. Hare, pers. obs.) and steadily lost mass over time, dying at three months of age.

Thirty-seven percent of juveniles born into the cohort were male, with 45% of twin clutches female, 22% male and 33% of mixed sexes. At birth, juveniles ranged in size from 29 to 35 mm SVL with one extremely small individual born at 26 mm SVL (Mean = 32.4 ± 0.5). Tail length at birth was similar to SVL ranging from 25 to 37 mm (Mean = 34.7 ± 0.6), and mass ranged from 0.6 to 1.1 g (Mean = 0.9 ± 0.1). There was no difference in any size measures (SVL, VTL, mass and BC) of male and female

		No. of nights in each plant species					Height above ground (m)	
Individı	ual No. nights tracked	Plant species	Leaves	Stems	Branches	Total	Mean ± SE	Range
1	8	Olearia paniculata	8	-	-	8	1.87 ± 0.03	1.7 - 2.0
2	7	O. paniculata	1	1	-	2	1 69 + 0 11	1.1 - 2.0
		Pittosporum tenuifolium	2	3	-	5	1.07 - 0.11	
3	7	Ozothamnus leptophyllus	3	-	-	3	0.54 ± 0.15	0.25 - 1.3
		Grass (spp. unknown)	-	-	-	4		
4	5	Olearia paniculata	2	-	-	2	1.80 + 0.07	1.55 - 2.0
		Coprosma repens	1	-	2	3	100 - 0107	
5	5	O. leptophyllus	4	-	-	4	0.17 ± 0.06	0 - 0.3
		Grass matrix	-	-	-	1		

Table 3. Nocturnal refuges used by five adult Naultinus manukanus during November 2004 on Stephens Island.

juveniles at birth or 6 mo of age (P > 0.05 for all measures). The SVL of mothers did not influence any size measures of juveniles at birth (P > 0.05), but mothers with lower BC immediately after parturition had juveniles with shorter SVL ($F_{1,17} = 8.528$, P < 0.01). However, the influence of maternal BC on juvenile size was not linear. A maternal BC index of -0.16 or lower produced significantly smaller offspring (range 26 to 31 mm SVL), whereas a maternal BC index of -0.12 or greater produced larger juveniles (32 to 37 mm SVL).

At six months of age juveniles ranged in size from 29 to 48 mm SVL (Mean = 45.2 \pm 0.3), 50 to 56 mm VTL (Mean = 53.2 \pm 0.5), and 1.8 to 2.5 g (Mean = 2.2 \pm 0.1). No size measures of mothers or initial size measures of juveniles influenced size measures at six months. Thus, the largest juveniles at birth were not necessarily the largest at 6 mo. Body condition did not differ significantly from birth to six months of age (Birth BC mean = 0.0 \pm 0.1; 6 month BC mean = 0.1 \pm 0.1; $F_{6, 105}$ = 1.166, P = 0.323). Growth was on average 0.07 \pm 0.03 mm/day to six months of age and did not differ between the sexes ($F_{1,15}$ = 0.682, P = 0.422), or with any other measure tested, including maternal BC (P = 0.077), maternal SVL (P = 0.699) or BC at birth (P = 0.978)

Discussion

We collated ecological and behavioural information from studies spanning 25 y of a viviparous, diurnal, cryptic green gecko, *N. manukanus*. Our study provides the first comprehensive ecological data on diurnal geckos from the family Diplodactylidae, as well as ecological and behavioural information vital for the conservation management of *Naultinus* geckos, especially as their habitats become more degraded and translocations of restricted populations increasingly necessary.

Natural population dynamics and seasonal changes

Over 25 y the population structure, traits and density of *N. manukanus* have remained stable despite an increase in available vegetation. The higher number of individuals captured in 2003 is a reflection of more available habitat and the longer transect searched. It is likely that revegetation of the island is providing more habitat and resources and enabling a larger population to be maintained, which is further supported by overall body condition of the population having less variation in 2002-2003 than 1978.

The female biased sex ratio of *N. manukanus* on Stephens Island has not altered over the 25 y study, and is similar to data from 1970 (1:1.6 M:F; A. Whitaker & Y. Werner unpubl. data). A female bias in sex ratio is apparent from birth, indicating that sampling bias (e.g., females basking more when pregnant), is not influencing the results. Sex ratios of geckos vary substantially among and within species. For example, studies on the nocturnal arboreal gecko *H. stephensi* and diurnal arboreal gecko *N. grayii* showed an adult sex ratio of approximately 1:1 M:F (Hitchmough 1982, Hare & Cree 2005). However, the nocturnal gecko *H. chrysosireticus* has an adult sex ratio of 1:2 M:F on Mana Island and of 1:0.5 M:F on mainland Taranaki (Flannagan 2000). Biased sex ratios of geckos may be a result of temperature-dependent sex determination (e.g., Tokunaga 1985, Tousignant & Crews 1995, Bragg *et al.* 2000). However, temperature-dependent sex determination in *N. manukanus* is unlikely as both sexes were present in 33% of clutches. The female biased sex ratio in this population may increase its reproductive potential, which is particularly important as not all females reproduce annually.

Wild-caught *N. manukanus* reach a maximum SVL of 81 mm, which is similar to previous unpublished accounts (Whitaker 1971, Hitchmough 1978), and show sexual size dimorphism, with females larger than males. However, the difference between the

size of males and females is minor as seen in other New Zealand geckos (e.g., *H. duvaucelii*, Barwick 1982). Data from the juveniles held in captivity indicate that males and females grow at the same rate until at least six months of age, at a rate similar to a wild population of *N. grayii* (0.09 mm per day (Hitchmough 1982) compared with 0.07 mm per day in *N. manukanus*). Because maternal body condition post-parturition, as opposed to snout-vent length, is the most important predictor of juvenile snout-vent length at birth it is unclear why females reach a larger size than males. Sex-biased predation may contribute to the size bias, but more research in this area is required.

Members of the New Zealand nocturnal gecko genus *Hoplodactylus*, which are the closest relatives of *Naultinus* geckos, have extreme longevity (e.g., up to 36 years in *H. duvaucelii* (Thompson *et al.* 1992) and *H.* aff. *maculatus* "Canterbury" (as *H. maculatus* in Bannock *et al.* 1999). There are no longevity estimates for natural populations of *Naultinus* geckos, and as no permanent marking of *N. manukanus* on Stephens Island was undertaken, longevity estimates were not possible in this study. However, in captivity *N. manukanus* live to at least 30 y (D. Keall, pers. comm.), and the closely related *N. stellatus* has been recorded at 47 y (H. Puklowski, pers. comm.). Future estimates of longevity in the wild may be possible as toe-clipped juveniles from this study were released on Whakaterepapanui Island, in the Marlborough Sounds, as part of the restoration goals for the island (Whitaker 2002).

The Stephens Island population of *N. manukanus* displays traits of slow growth and low reproductive output, which are consistent with many other small New Zealand reptile species (e.g., Barwick 1982, Cree 1994, Cree & Guillette 1995, Hare & Cree 2005), but not with many other lizard species world wide (e.g., Cree 1994, Harlow & Taylor 2000, Chapple 2003). The low reproductive output of *N. manukanus* and other New Zealand fauna make them especially vulnerable to predation by exotic mammals, and are implicated in the decline of many species (e.g., Holdaway 1989, Daugherty *et al.* 1993, Cree 1994).

Habitat use and daily movement patterns

Naultinus manukanus is an arboreal species that routinely uses foliage of a wide range of coastal shrub and tree species on Stephens Island. It appears to use introduced grasses and other low vegetation only whilst in transit between shrubs and trees in regenerating forest areas. Limited use of grasses and other low vegetation supports the hypothesis that habitat modification on the adjacent South Island has created suboptimal habitat, which can only support geckos at low density (Whitaker & Gaze 1999). However, individuals will disperse across non-forested areas (Whitaker 1971; this study). *Naultinus manukanus* is likely to benefit from the ecological restoration programme on Stephens Island, as shrubby vegetation increases and reconnects patches of remnant coastal forest.

A disproportionate number of *N. manukanus* captures were on the coastal shrub *O. leptophyllus*, which has often been attributed to the contrast of brightly coloured green geckos on the dull grey-green foliage and may have reflected observer biases rather than actual habitat use. However, our telemetry study demonstrates that geckos use this vegetation disproportionately to its availability during spring (Fig. 2). *Ozothamnus leptophyllus* is predominantly located in areas of regeneration, where lizards occur in high densities on Stephens Island (East *et al.* 1995, Stephens 2004), and where the radio-telemetry study was undertaken. The only species that is more often used is *O. paniculata*, in which these geckos are well camouflaged.

Naultinus geckos appear to use structurally diverse scrub habitats (Whitaker 1971, Hitchmough 1982; this study). Our *N. manukanus* habitat data can be used to direct search effort at mainland sites to aid current conservation management practices, which include both species monitoring and obtaining individuals for translocations to mammal-free sites. However, we caution that *N. manukanus* is not confined to coastal shrub and tree species on the mainland (Whitaker and Gaze, 1999) where it faces the added pressures of habitat destruction and mammalian predation. The differences in habitat availability and predation pressures in mainland populations may result in behavioural differences, including habitat use changes, and warrant further investigation.

Naultinus manukanus is strictly diurnal, which is consistent with findings for physiological studies on daily rhythms of metabolic rate (Hare *et al.* 2006) as well as behaviour of congeneric *N. gemmeus* (Salmon 2002). Both hourly and daily movements of *N. manukanus* are limited and consistent with other known traits of these geckos, including cryptic colouration and secretive behaviour (Whitaker 1994). They appear to use a sit-and-wait mode of foraging, rather than actively seeking food. Less movement of geckos is observed during cloudy conditions, demonstrating that geckos use direct sunlight for thermoregulation and other activity. The geckos are frequently observed basking in direct sunlight, and have been observed actively moving into sunlight to bask (Werner & Whitaker 1978; this study). We found that although geckos did not actively track the sun, they did emerge opportunistically when the sun shone on the vegetation in which they were located. *Naultinus manukanus* may not require thermoregulatory opportunities as frequently as other diurnal lizards, as indicated by their low thermal sensitivity of metabolic rate when compared to other diurnal lizards (Hare *et al.* 2006).

Nocturnal locations

The eight individuals captured at night during March 2003 were not active and were all located deep in the foliage, but after registering our presence did try to evade capture. In contrast, the nocturnal species *H. stephensi* and *H. maculatus* were actively

foraging at this time and were found on the outside of vegetation (Hare & Cree 2005, Hoare & Nelson 2006). These observations are further supported by the telemetric study, in which only two instances of limited movement were recorded for *N*. *manukanus* at night.

Naultinus manukanus did not overnight at consistent sites, implying that nocturnal retreat sites are not used, at least during spring. Retreat sites may be used at other times of the year and require further investigation. Instead, geckos appeared to spend the night wherever they were located when the sun moved off them, but generally moved deeper within the foliage. As these cryptically coloured geckos were usually concealed amidst foliage at night, and were typically above ground, their choice of nocturnal sites may enable them to avoid native, primarily visual predators (e.g., tuatara, *Sphenodon punctatus*, which are medium-sized, nocturnal, ground-dwelling reptilian predators and nocturnal birds such as owls, *Ninox novaezealandiae*). On New Zealand's main islands, where introduced mammalian predators include commensal rodents (*Mus musculus* and *Rattus* spp.) and mustelids (*Mustela* spp.) the lack of use of protected nocturnal retreat sites may increase their vulnerability to predation. However their arboreal position and the narrowness of the branches among which they sit would reduce their accessibility to many predators.

Conservation management

The long-term prospects for *N. manukanus* on Stephens Island appear good. They are legally protected, use new habitat as it becomes available, and population structure and density is stable. However, populations on the mainland are at high risk from habitat destruction, predation and competition with exotic species (Thomas 1987, Whitaker & Gaze 1999). The threats on the mainland are further amplified by their extremely K-selected life history strategies, including low reproductive output and

extended time to reach maturity (Cree 1994; this study). Also, due to their limited movement patterns, the relictual, fragmented populations on the mainland may have limited gene flow, which will have implications for genetic integrity of the populations (Mills & Allendorf 1996).

Data on the mainland populations of *N. manukanus* are scarce, but decline of other *Naultinus* populations indicates that all *Naultinus* species are under threat and require immediate conservation intervention. For example, the *N. gemmeus* population at Every Scientific Reserve on the Otago Peninsula declined by 50% over a seven year period from 1994-2001 (Schneyer 2001). Similar declines of other *Naultinus* populations on the mainland are common throughout New Zealand (Hitchmough 2002). These trends are worrying, especially as *Naultinus* species have historically not been thought to be at risk as they were not restricted to islands like many other lizard species (Daugherty *et al.* 1994). Now many *Naultinus* species are classed as 'gradually declining' by the New Zealand Department of Conservation (Hitchmough 2002).

The life-history strategy of *Naultinus* geckos means that conservation management requires either intensive management of predators and competitors at currently populated mainland sites to allow population densities to increase and attain stability, or translocation to mammal-free offshore islands with appropriate vegetative cover. The first step towards safe havens for a few *Naultinus* species have begun, with translocation of *N. manukanus* from Stephens Island to nearby Whakaterepapanui Island, and of *N. elegans punctatus* from mainland Wellington to Mana Island (Miskelly 1999).

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APPENDIX 2

The impact of brodifacoum on non-target wildlife: gaps in knowledge¹

Abstract

Anticoagulant poisons, especially the second-generation anticoagulant brodifacoum, are used worldwide to eradicate pest mammals from high priority nature sites. However, the potency and persistence of brodifacoum may present threats to nontarget species. In New Zealand, most ecosystems lack native terrestrial mammals; instead, birds, reptiles and invertebrates fulfil key ecosystem roles. Introduced mammals represent the biggest threat to persistence of native species. Therefore, in addition to use in eradications, brodifacoum is often continuously supplied in ecosystems for pest mammal control and detection of mammalian reinvasions, creating a potential long-term risk of poisoning to non-target species. We reviewed literature concerning brodifacoum effects on non-target native fauna in New Zealand as a framework for discussing current research requirements. Birds and their invertebrate prey have, to date, been the focal taxa of such empirical studies (26 species and 11 orders studied, respectively). Brodifacoum is linked to both mortality and sub-lethal contamination in native birds, and the toxicant is consumed by a range of native invertebrates. Reptiles, amphibians, bats and aquatic invertebrates are considered at low risk of anticoagulant poisoning and are not routinely included in risk assessments.

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However, recent field evidence demonstrates that native geckos consume brodifacoum bait. Reptiles are often abundant on mammal-free offshore islands where brodifacoum is used persistently as a simultaneous rodent detection and killing strategy. Ectothermic vertebrates, though at low risk of toxicosis themselves, may act as vectors of brodifacoum and create a risk of secondary poisoning to native birds. The effectiveness of using poison bait to protect mammal-free ecosystems is uncertain, due to the abundance of alternative food supplies available to an invading rodent. However, where sustained brodifacoum use is deemed appropriate, the role of reptiles as consumers and vectors of anticoagulant poison should be a research priority.

Introduction

Introduced mammalian predators have caused catastrophic declines or extinctions of many species world-wide (Case & Bolger 1991). Thus, eradication and control of mammalian pests have been necessary in order to protect native biodiversity (e.g., Innes & Barker 1999, Atkinson 2001, Towns & Broome 2003). Anticoagulant toxins (particularly the second-generation poison brodifacoum) are powerful conservation tools for poisoning rodents and other vertebrate pests (e.g., Donlan *et al.* 2003). Use of anticoagulants has increased world-wide (e.g., Godfrey 1985), and is currently the most commonly used method of pest-mammal eradication (Stone *et al.* 1999, O'Connor & Eason 2000, Towns & Broome 2003). While using brodifacoum to eradicate mammals poses a risk to non-target native species through primary and secondary poisoning, the benefits of eradication usually outweigh costs (Innes & Barker 1999). However, concerns about brodifacoum persistence and potency have resulted in restrictions on its use in many parts of the world (e.g., field use is banned in the United States of America; Stone *et al.* 1999).

Brodifacoum is a potent rodenticide that binds strongly to vitamin K epoxide reductase and persists for at least six months in organs and tissue containing this enzyme, such as the liver, kidney and pancreas (Stone *et al.* 1999, Eason *et al.* 2002). The persistence of brodifacoum in tissue exacerbates the risk of secondary poisoning of non-target species (Eason *et al.* 1996; Eason & Wickstrom 2001, Eason *et al.* 2002), and poses a clear risk to avian predators and scavengers (e.g., Mendenhall & Pank 1980, Howald *et al.* 1999). A lethal dose (LD₅₀) in birds is usually 3–20 mg/kg (compared with <1 mg/kg in target mammals), though some bird species are highly susceptible (e.g., pukeko, *Porphyrio porphyrio melanotus*, has a LD₅₀ of ≤1 mg/kg; Eason & Spurr 1995a).

New Zealand as a case study for investigating the non-target effects of brodifacoum

Native mammals are extremely widespread on a global scale. Therefore, eradicating pest mammals for conservation frequently encounters the problem of simultaneously protecting non-target native mammals. As such, global research effort into the effects of brodifacoum on non-target species has focused on the risks of primary consumption to native mammals, and of secondary poisoning to large predatory birds (e.g., Howald *et al.* 1999, Shore *et al.* 1999, Burn *et al.* 2002, Brakes & Smith 2005). However, targeting these species for research may obscure patterns of anticoagulant poison transport through a native ecosystem as other potential pathways, especially via native vectors, are not considered.

New Zealand's fauna evolved in isolation from terrestrial mammals (apart from bats, King 1990). Recent mammalian introductions have resulted in many extinctions and declines of native populations not adapted to mammalian predation (e.g., Cassels

1984, Towns & Daugherty 1994). However, the lack of native mammalian fauna also means that use of anticoagulant poisons as a conservation tool has been a viable, successful and widely used option (e.g., Dilks & Towns 2002). Monitoring of nontarget species following brodifacoum-mediated mammal eradications in New Zealand provides much of the current knowledge on the effects of second-generation anticoagulant poison on non-target wildlife.

Mammal eradication and control programmes in New Zealand provide an opportunity for long-term research into non-target effects of anticoagulant poisons and inform vertebrate pest control operations world-wide. However, we suggest that research on non-target effects of anticoagulant poison use in the wild is taxonomically unrepresentative, which is of concern to native (i.e., mammal-free) ecosystems particularly where poison is continually available (Hoare & Hare 2006, reprinted in Appendix 3). In the present paper we synthesise existing information on the effects of brodifacoum on non-target species in the wild, using a literature review of New Zealand-based research as a case study. We aim to determine the status of knowledge about toxic effects of brodifacoum in native ecosystems and to recommend future research directions.

Patterns of brodifacoum use in New Zealand

Anticoagulant poisons have been used as a conservation tool in New Zealand to achieve mammal eradication, control and detection of reinvasion (Dilks & Towns 2002, Towns & Broome 2003). Aerial distribution of brodifacoum has been a key tool in eradication of mammals from key offshore islands targeted for conservation and ecological restoration (Towns & Broome 2003). Brodifacoum is one of five pesticides currently registered for rodent control (O'Connor & Eason 2000). In mammal-control operations, and as a means of simultaneously detecting and killing invading rodents (termed 'island protection'), brodifacoum bait is replenished on a regular and continuous basis to bird-excluding bait boxes (Dilks & Towns 2002).

We conducted a survey of major pest control companies, the New Zealand Department of Conservation (DoC) pest control staff from all 13 Conservancies, and all Regional Councils to investigate patterns of brodifacoum use in New Zealand. An estimated 6 kg of pure brodifacoum active ingredient are contained within all of the brodifacoum products sold in New Zealand each year (B. Simmons, Animal Control Products Ltd, Wanganui, N.Z., pers. comm.). Of the brodifacoum sold, ca. 50% is used by private contractors. Other users are Regional Councils (ca. 30%), DoC (ca. 15%; mostly in eradication operations) and private landowners (ca. 5%; B. Simmons, pers. comm.).

Private contractors use brodifacoum as one of a variety of tools, mostly in bovine tuberculosis (Tb) vector (possum and ferret) control in New Zealand. The company Epro Ltd alone is responsible for pest control over 780 000 ha of the North Island, and estimates that brodifacoum is used across 20% of this area (C. Speedy, Epro Ltd, Taupo, N.Z., pers. comm.).

Regional Councils use brodifacoum principally in protection of sites identified as 'Key Native Ecosystems' and as a mechanism to control possums, as vectors of Tb. Sustained brodifacoum use continues in some areas to protect threatened native fauna. For example, in the Auckland Region, brodifacoum has been used in ongoing mammal control operations in an 850 ha area in the Hunua kokako (*Callaeas cinerea wilsoni*) management area (12 years to date) and in the 80 ha Wenderholm Regional Park (to protect North Island robins, *Petroica australis longipes*; 11 years to date; DoC, 2005; Lovegrove *et al.* 2002). Brodifacoum has been an effective tool in possum control to minimise spread of Tb in many regions. For example, of the 1 000 000 ha of Animal Health Board funded possum control in the Manawatu/Wanganui Region, 300 000 is under a brodifacoum-bait station programme (C. Mitchell, Animal Pest Unit, Horizons Regional Council, Palmerston North, N.Z., pers. comm.). A further 70 000 ha of private possum control using brodifacoum is supported by the Regional Council, and an estimated 150 tonnes of brodifacoum is used in the region annually (C. Mitchell, pers. comm.).

A policy on use of second generation anticoagulant poisons on public conservation land (DoC, 2000) in response to concerns over bioaccumulation of anticoagulant poisons and associated risk to non-target fauna has resulted in reduction of their use by DoC at mainland sites (DoC, 2005). Anticoagulant poisons, particularly brodifacoum, are used to control mammals at a few key mainland sites in most conservancies to protect threatened fauna (DoC, 2005). For example, in the Hawdon, Hurunui and Poulter catchments, Canterbury, brodifacoum is used in an attempt to protect orange-fronted parakeets, *Cyanoramphus malherbi* (DoC, 2005; S. Hooson, DoC, Christchurch, N.Z., pers. comm.). The policy does not affect anticoagulant poison use on offshore islands, and brodifacoum is used frequently in a sustained manner for protection of islands considered to be key ecological sites and visited regularly (DoC, 2005). For example, the Sugar Loaf Islands in the Wanganui Conservancy and Kapiti, Mana and Matiu Islands in the Wellington Conservancy are protected by sustained brodifacoum baiting (Williams 2003; DoC, 2005).

Overall, brodifacoum is the key poison that has enabled eradication of mammals from many offshore islands of conservation importance (Towns & Broome 2003). Brodifacoum baiting is one of a number of strategies used in a sustained manner for widespread pest control in New Zealand. Although use in the conservation estate has decreased since 2000 due to concerns over the persistence of brodifacoum (DoC, 2000), it continues to be used in island protection strategies (Dilks & Towns 2002). As sustained use of brodifacoum forms part of key strategies to protect native wildlife and reduce the spread of Tb, its use is likely to continue in the foreseeable future.

Sources of information about non-target impacts of brodifacoum

Our literature review of journal publications, theses and technical reports (Table 1) demonstrates that information about non-target effects of brodifacoum poison comes primarily from eradication operations, where poison is distributed in a single event. It has also been collected opportunistically, following the environmental contamination caused by a recent spill of 20 tonnes of brodifacoum bait into the ocean (Pestoff[®]; Primus et al. 2005). Relatively little research has been based on monitoring of sustained anticoagulant use, despite it being common in long-term pest control and in detection of rodent invasions (O'Connor & Eason 2000, Dilks & Towns 2002, Roberts 2003). Even among studies that use pest control operations as a means of investigating non-target effects of brodifacoum, long-term monitoring of the impacts of poison in native systems is rare. Of the seven studies that have investigated non-target effects of brodifacoum in New Zealand (categories 'C' and 'IP' in Table 1), only one has involved following potential non-target consumers of the toxin for more than three months (Robertson et al. 1999). Robertson et al. (1999) monitored the effects of sustained exposure to brodifacoum poison in brown kiwi, Apteryx mantelli, for up to 32 months. Knowledge from long-term studies would greatly enhance risk management assessments concerning sustained brodifacoum use.

Empirical research into the non-target effects of anticoagulant poisons to native ecosystems has often occurred on a species-by-species basis, despite recent theoretical discussion about ecosystem-level impacts (Innes & Barker 1999) and demonstration of secondary poisoning of non-target species in a mammalian food chain (Alterio 1996). **Table 1.** Non-target native animal taxa studied in the wild in relation to potential brodifacoum poisoning in New Zealand. We define mortality as confirmed death of at least one individual from brodifacoum poisoning. E = eradication; C = control; IP = island protection; S = accidental spill; $1^{\circ} = primary poisoning$; $2^{\circ} = secondary poisoning$; Y = yes; N = no; ? = unknown; • indicates presence in a category; \circ indicates inferred by primary authors to be in category; * indicates that the study includes observational data only. Note that brodifacoum content is 50 ppm in Talon 50 WB, and 20 ppm in all other bait types.

Non-target native species monitored	Location (eradication, control or island protection operation)	Brodifacoum-based bait type	Brodifacoum residue or observed bait consumption			Level of consumer			Mortality?			References
			Y	Ν	?	1°	2°	?	Y	Ν	?	
BIRDS												
Anas platyrhyncos (mallard duck)	Motuihe Island (E)	Talon 7-20 ®	•					•	•			Dowding et al. 1999
A. superciliosa (grey duck)	Motuihe Island (E)	Talon 7-20 ®	•					•	•			Dowding et al. 1999
Anthornis melanura (bellbird)	King Country (C)	Talon 50 WB		•						•		Murphy et al. 1998
	Nelson Lakes (C)	Talon 20WP TM		•						•		Spurr et al. 2005
Apteryx australis (brown kiwi)	Northland (C)	Talon 20P ®; Pestoff ®	•					•	•			Robertson et al. 1999
A. owenii (little spotted kiwi)	Red Mercury Island (E)	Talon 20P ®		•						•		Robertson et al. 1993
· · ·	Kapiti Island (E)	Wanganui No. 7	•			•					•	Empson & Miskelly 1999
Callaeas cinerea (kokako)	Kapiti Island (E)	Wanganui No. 7			•						•	Empson & Miskelly 1999
<i>Charadrius obscurus</i> (New Zealand dotterel)	Motuihe Island (E)	Talon 7-20 ®		•						٠		Dowding et al. 1999
<i>Circus approximans</i> (Australasian harrier)	Canterbury (C)	Mapua	•				0		•			Rammell <i>et al.</i> 1984, Williams <i>et al.</i> 1986
	King Country (C)	Talon 50 WB		•						•		Murphy et al. 1998
	Motuihe Island (E)	Talon 7-20 ®	•					•	•			Dowding et al. 1999
Cyanoramphus novaezelandiae (red- crowned kakariki)	Lady Alice Island (E)	Talon 20P ®	•					•	•			Ogilvie et al. 1997
Cyanoramphus spp (kakariki)	Nelson Lakes (C)	Talon 20WP TM		•						•		Spurr et al. 2005
Gallirallus australis (weka)	Tawhitinui Island (E)	Talon ® 50WB	•			•			•			Taylor 1984
	Kapiti Island (E)	Wanganui No. 7	•			•			•			Empson & Miskelly 1999
	Nelson Lakes (C)	Talon 20WP TM	•					•		٠		Spurr et al. 2005
Haematopus unicolor (variable	Motuihe Island (E)	Talon 7-20 ®		•						٠		Dowding et al. 1999

oystercatcher)

Table 1 continued

Non-target native species monitored	species monitored Location (eradication, control Brodifacoum-based Brodifacoum		ım	Level of			Mortality?			References		
	or island protection operation)	bait type	residue or observed		co	nsume	r					
			Y	N	?	1°	2°	?	Y	N	?	-
Larus bulleri (black-billed gull)	Nelson Lakes (C)	Talon 20WP TM	•			-	_	•			•	Spurr et al. 2005
L. dominicanus (southern black-	Canterbury (C)	Mapua	•				0	-	•		-	Rammell <i>et al.</i> 1984, Williams
backed gull)		F										<i>et al.</i> 1986
	Motuihe Island (E)	Talon 7-20 ®	•					•	•			Dowding et al. 1999
Mohoua albicilla (whitehead)	King Country (C)	Talon ® 50WB		•						•		Murphy et al. 1998
Nestor meridionalis (kaka)	Whatupuke Island (E)	Wanganui No. 7;			•					•		Pierce & Moorhouse 1994
		Talon 20P ®										
	Nukuwaiata Island (E)	Talon 7-20 ®		0		0				•		Brown 1997a
	Kapiti Island (E)	Wanganui No. 7	•					•	•			Empson & Miskelly 1999
	Nelson Lakes (C)	Talon TM	٠					•	•			Moorhouse et al. 2003
	Nelson Lakes (C)	Talon 20WP TM	•					•	0			Spurr et al. 2005
N. notabilis	Nelson Lakes (C)	Talon 20WP TM	•					•		•		Spurr <i>et al.</i> 2005
Ninox novaeseelandiae (morepork)	Lady Alice Island (E)	Talon 20P ®	٠				•				٠	Ogilvie et al. 1997
	Nukuwaiata Island (E)	Wanganui No. 7	٠				•		•			Walker & Elliott 1997
	King Country (C)	Talon ® 50WB	٠				•				٠	Murphy et al. 1998
	Kapiti Island (E)	Wanganui No. 7	•				•		•			Empson & Miskelly 1999
	Mokoia Island (E)	Talon 7-20	٠				•		•			Stephenson et al. 1999
	Nelson Lakes (C)	Talon 20WP TM	٠					•			٠	Spurr et al. 2005
Petroica australis (robin)	King Country (C)	Talon ® 50WB		•						٠		Murphy et al. 1998
	Kapiti Island (E)	Wanganui No. 7	•			•			0			Empson & Miskelly 1999
<i>P. australis australis</i> (South Island	Breaksea Island (E)	Talon ® 50WB			•	0				•		Taylor & Thomas 1993
100111)	Maruia (C)	Talon 20P ®	0			Ō			0			Brown 1997h
	Nelson Lakes (C)	Talon 20WP TM	•			0		•	0		•	Spurr et al. 2005
P macrocenhala (tomtit)	King Country (C)	Talon ® 50WB	•	•				•		•	•	Murphy et al. 1998
1. macrocepnaia (tolliat)	Nelson Lakes (C)	Talon 20WP TM		•								Spurr et al. 2005
Philesturnus carunculatus	Red Mercury Island (F)	Talon 2000 ®	•	•				•	•	•		Towns et al. 1994
(saddleback)	Red Wereury Island (L)		·					•	•			10 wils et al. 1774
	Kapiti Island (E)	Wanganui No. 7	•			٠					٠	Empson & Miskelly 1999
Porphyrio p. melanotus (pukeko)	Motuihe Island (E)	Talon 7-20 ®	٠					٠	•			Dowding et al. 1999
Prosthemadera novaeseelandiae (tui)	Nelson Lakes (C)	Talon 20WP ^{1M}		•						٠		Spurr <i>et al.</i> 2005
Rhipidura fuliginosa (fantail)	King Country (C)	Talon ® 50WB		٠						•		Murphy et al. 1998
	Nelson Lakes (C)	Talon 20WP TM		•						٠		Spurr <i>et al.</i> 2005
<i>Tadorna variegata</i> (paradise shelduck)	Canterbury (C)	Mapua	•			0			•			Rammell et al. 1984, Williams et al. 1986
	Motuihe Island (E)	Talon 7-20 ®	٠					•	•			Dowding et al. 1999

Table 1 continued

Non-target native species monitored	Location (eradication, control or island protection operation)	Brodifacoum-based bait type	Brodifacoum residue or observed bait consumption		Level of consumer			Mortality?			References	
		T I AOUTTM	Y	N	?	1°	2°	?	Y	N	?	<u> </u>
Zosterops lateralis	Nelson Lakes (C)	Talon 20WP TM	•					•			•	Spurr <i>et al.</i> 2005
FISH												
Notolabrus celidotus (spotty)	Kapiti Island (E)	Wanganui No. 7			•			•			٠	Empson & Miskelly 1999
Odax pullus (butterfish)	Kaikoura (S)	Pestoff®	•			0				٠		Primus et al. 2005
Scorpaena papillosus (scorpion fish)	Kaikoura (S)	Pestoff®	•			0				•		Primus et al. 2005
Sprattus sp. (herring)	Kaikoura (S)	Pestoff®	•			0				٠		Primus et al. 2005
INVERTEBRATES aquatic												
Cellana ornata (limpets)	Kaikoura (S)	Pestoff®	•					•		•		Primus et al. 2005
Coscinaterias muricata (starfish)	Kaikoura (S)	Pestoff®	•					•		•		Primus et al. 2005
Evechinus chloroticus (sea urchin)	Kaikoura (S)	Pestoff®	•					•		•		Primus et al. 2005
Haliotis iris (abalone)	Kaikoura (S)	Pestoff®	•					•		•		Primus et al. 2005
Jasus sp. (rock lobster)	Kaikoura (S)	Pestoff®	٠					٠		٠		Primus et al. 2005
Mytilis edulis (blue mussels)	Kaikoura (S)	Pestoff®	٠			0				٠		Primus et al. 2005
Perna canaliculus (green lip mussels)	Kaikoura (S)	Pestoff®	٠			0				•		Primus et al. 2005
INVERTEBRATES terrestrial												
Araneae (spider)	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		•		Morgan et al. 1997
Blattodea (cockroaches)	Lady Alice Island (E)	Talon 20P ®	0			•					٠	Ogilvie et al. 1997
	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		٠		Morgan et al. 1997
Coleoptera (black beetles)	Lady Alice Island (E)	Talon 20P ®	0			•					٠	Ogilvie et al. 1997
	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		٠		Morgan et al. 1997
Chilopoda (centipede)	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		٠		Morgan et al. 1997
Diplopoda (millipede)	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		٠		Morgan et al. 1997
Gastropoda (slugs)	Red Mercury Island (E)	Talon ® 50WB	•					٠			٠	Morgan et al. 1997

Table 1 continued

Non-target native species monitored	Location (eradication, control or island protection operation)	Brodifacoum-based bait type	Brodifacoum residue or observed bait consumption			Level of consumer			Mortality?			References
			Y	Ν	?	1°	2°	?	Y	Ν	?	
Gastropoda (snails)	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		•		Morgan et al. 1997
Hymenoptera (ants and wasps)	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		•		Morgan et al. 1997
Huberia brouni (ant)	West Coast (C)	No. 7, AgTech	0			•					•	Spurr & Drew 1999
Prolasius advena (ant)	West Coast (C)	No. 7, AgTech	0			•					•	Spurr & Drew 1999
Isopoda (slater)	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		•		Morgan et al. 1997
Opisthopora (worm)	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		٠		Morgan et al. 1997
Orthoptera (weta)	Red Mercury & Coppermine Islands (E)	Talon ® 50WB		•				•		•		Morgan et al. 1997
<i>Gymnoplectron</i> sp.	West Coast (C)	No. 7, AgTech	0			•					٠	Spurr & Drew 1999
	Lady Alice Island (E)	Talon 20P ®	•			•					•	Ogilvie et al. 1997
Hemideina crassidens	West Coast (C)	No. 7, AgTech	0			•					•	Spurr & Drew 1999
H. thoracica	Lady Alice Island (E)	Talon 20P ®			•						•	Ogilvie et al. 1997
Isosplectron sp.	West Coast (C)	No. 7, AgTech	Ō			•					•	Spurr & Drew 1999
Pleioplectron sp.	West Coast (C)	No. 7, AgTech	0			•					٠	Spurr & Drew 1999
Talitropsis sp.	West Coast (C)	No. 7, AgTech	0			•					٠	Spurr & Drew 1999
Weta sp.	West Coast (C)	No. 7, AgTech	Ō			•					•	Spurr & Drew 1999
Zealandosandrus sp.	West Coast (C)	No. 7, AgTech	0			•					٠	Spurr & Drew 1999
Zealandosandrus aff. gracilis	West Coast (C)	No. 7, AgTech	0			•					٠	Spurr & Drew 1999
REPTILES AND AMPHIBIANS												
Hoplodactylus duvaucelii (Duvaucel's gecko)	Lady Alice Island (E)	Talon 20P ®	•			•				•		Christmas 1995 *
H. maculatus (common gecko)	Mana Island (IP)	Pestoff ®	•			•					•	Appendix 3*

Current methods of evaluating non-target impacts rely on information about toxic brodifacoum residues in the livers of dead animals collected from within the vicinity of the poison drop (e.g., Rammell *et al.* 1984, Ogilvie *et al.* 1997, Robertson *et al.* 1999). This approach enables the identification of species at risk of mortality and sub-lethal contamination in poisoning operations, and the establishment of likely pathways of poison through an ecosystem. However, it does not allow quantification of either the relative importance of different vectors of brodifacoum, or the risk posed to non-target wildlife by a brodifacoum poisoning operation relative to its dosage and longevity.

Current knowledge of non-target effects of brodifacoum use in New Zealand

Birds and terrestrial invertebrates have been focal taxa in evaluations of non-target impacts of brodifacoum (Table 1). The effects of brodifacoum use have been studied in relation to 26 bird species, four fish species, seven aquatic invertebrate species and 11 terrestrial invertebrate orders and brodifacoum bait consumption has been noted in two reptile species. However, there are no post-baiting monitoring data on amphibians, reptiles, bats or parasites of these taxa (though Eason & Spurr 1995b assess the theoretical risk to bats).

Of New Zealand's 53 extant native terrestrial bird species (Atkinson & Millener 1991), 22 have been studied in relation to non-target effects of brodifacoum (Table 1). Seabirds are not so well represented in the literature: four of 75 extant species (Turbott 1990) have been studied (Table 1). The lethal effects of brodifacoum to native shorebirds have been confirmed in northern New Zealand dotterels, *Charadrius obscurus acquilonius*, and observed in a further two species, pied stilts, *Himantopus himantopus*, and spur-winged plovers, *Vanellus miles novaehollandiae*, following a mainland island mammal eradication attempt at Tāwharanui Regional Park, Auckland

(J. Dowding, DM Consultants, Christchurch, unpubl. data). However, non-avian taxa have received very little attention. For example, although New Zealand has 82 native reptile species (Hitchmough *et al.* 2005) reports of brodifacoum consumption are only known for two species (Christmas 1995).

Brodifacoum has been implicated in lethal primary and secondary poisoning and sub-lethal contamination of non-target native species in New Zealand (Table 1). The only known non-target deaths caused by brodifacoum poisoning are in birds. In an extreme case, a flightless bird population (the western weka, *Gallirallus australis australis*) was extirpated from Tawhitinui Island, Marlborough Sounds, by primary and secondary consumption of Talon ® 50WB targeted at ship rats, *Rattus rattus* (Taylor 1984). However, most eradications facilitated by the use of brodifacoum poisoning result in much smaller bird population die-backs (Table 1). Brodifacoum is known to have lethal consequences for 16 non-target native New Zealand bird species, and another 12 species are considered at risk of dying following pest control operations (Eason *et al.* 2002).

Concerns that invertebrate populations are susceptible to poisoning from vertebrate pest control and eradication operations have led to a number of studies in recent years (Spurr & Drew 1999, Booth *et al.* 2001; Table 1). Although we have found no records of lethal impacts of brodifacoum poisoning for insects, a wide variety of aquatic and terrestrial invertebrates are known to consume toxic brodifacoum pellets (Table 1; Pain *et al.* 2000).

The only information about interactions between brodifacoum poison and native reptiles is observational, confirming brodifacoum consumption by two New Zealand gecko species (Christmas 1995). Common geckos, *Hoplodactylus maculatus*, on Mana Island, eastern Cook Strait, show evidence of bait consumption where brodifacoum (Pestoff ®) is continuously supplied in bait stations as a strategy to simultaneously

detect and kill invading rodents (Appendix 3). Similarly, bait consumption (Talon 20P (®) by a single Duvaucel's gecko, *Hoplodactylus duvaucelii*, was discovered on Lady Alice Island, Hen and Chickens Group, Northland, following rodent eradication (Christmas 1995).

Potential vectors of brodifacoum through a native ecosystem

On a global scale, discussions concerning the risk of secondary poisoning to nontarget native species have focussed on target (i.e., mammalian) prey species as vectors for anticoagulant transportation (e.g., Eason & Wickstrom 2001). However, over the past decade, non-target (mostly invertebrate) consumers of toxins have also been the focus of research assessing the non-target impacts of anticoagulant poisons (e.g., Morgan *et al.* 1997, Ogilvie *et al.* 1997, Spurr & Drew 1999, Pain *et al.* 2000).

Invertebrates consume anticoagulant bait (Ogilvie *et al.* 1997, Spurr & Drew 1999) but do not have the same blood clotting systems as vertebrates (Shirer 1992, Morgan *et al.* 1997) and are therefore thought to be at low risk of toxicosis from ingesting brodifacoum (e.g., Morgan & Wright 1996). However, recent evidence demonstrates lethal consequences even at low doses in some molluscs (Gerlach & Florens 2000). Two snail species, *Pachnodus silhouettanus* and *Achatina fulica*, from Frégate Island, Seychelles suffered mortality as a result of exposure to doses of 0.01 to 0.2 mg and 0.04 mg of brodifacoum, respectively, over a 72–h period and brodifacoum is likely to be lethal to another snail, *Pachystyla bicolor*, from Mauritius (Gerlach & Florens 2000, Booth *et al.* 2001). Although brodifacoum-related primary poisoning of native *Powelliphanta* species in New Zealand is considered unlikely, native snails may be at risk of secondary poisoning through consumption of other invertebrates (Booth *et al.* 2003). Brodifacoum residues of up to 7.47 μg/g have been recorded in native

terrestrial invertebrates (Craddock 2003). Residue levels take in excess of four weeks to return to background levels, and trace levels are detectable up to ten weeks following brodifacoum baiting operations, which poses a risk to native insectivorous bird species and possibly molluses (Booth *et al.* 2003, Craddock 2003).

The potential risk of brodifacoum poisoning to ectothermic vertebrates (reptiles and amphibians) is also considered to be low, as they have a distinct blood coagulation chemistry to that of mammals (Merton 1987). However, few studies world-wide have investigated whether reptiles consume anticoagulant bait (exceptions are Merton 1987, Freeman *et al.* 1996, Thorsen *et al.* 2000) or have sufficient data on reptiles to indicate consumption (Empson & Miskelly 1999).

Reptiles are an important component of some New Zealand food webs, especially on mammal-free offshore islands where they are abundant (Daugherty *et al.* 1990, Heather & Robertson 1996, Keall *et al.* 2001, Towns 2002) and at some mainland locations (Towns 1996). However, despite observational (Christmas 1995) and laboratory (Freeman *et al.* 1995, 1996) evidence indicating that New Zealand lizards consume anticoagulant baits, the potential role of reptiles as vectors for transport of toxin through a natural food web is rarely considered (but see Innes & Barker 1999 for a theoretical discussion). Even on a global scale information about interactions between reptiles and brodifacoum world-wide is sparse. We found only two reports of the impacts of brodifacoum on reptiles: toxic bait consumption has been reported in Telfair's skink, *Leiolopisma telfairi*, from Round Island, Mauritius (Talon 20P ®; which proved lethal in some individuals; Merton 1987, Merton 1988, Merton *et al.* 2002) and Wright's skink, *Mabuya wrightii*, from Frégate Island, Seychelles (Talon 50 WBTM; Thorsen *et al.* 2000).

Lethal doses of anticoagulant poison for reptiles are not known. Hypothesised sub-lethal effects of brodifacoum include interference with reptiles' abilities to

thermoregulate, which may prove fatal under conditions of environmental stress (Merton 1987). However, the main risk associated with reptiles consuming anticoagulant baits is likely to be secondary poisoning of their native avian predators.

To date, focal taxa for investigations into non-target effects of brodifacoum on wildlife have been birds and terrestrial invertebrates. In mammal-free systems where brodifacoum is used continuously to detect rodent invasions, native ecosystems contain a more representative suite of native fauna. In such systems, native taxa, such as reptiles, occur at densities that enable them to play a functional role in ecosystems (Towns 1991, 2002).

Current research does not enable assessment of the roles that various trophic groups play in food (and hence poison) pathways through these ecosystems. Bioaccumulation of persistent toxins such as brodifacoum puts top consumers most at risk of secondary poisoning (Eason *et al.* 1996; Eason & Wickstrom 2001, Eason *et al.* 2002). Native invertebrate consumers of brodifacoum bait (Ogilvie *et al.* 1997, Spurr & Drew 1999), though not known to suffer mortality from the toxin, may pose a risk of secondary poisoning to their avian predators (Craddock 2003), both directly and via reptiles as an intermediate vector. Additionally, reptiles may be significant direct vectors of brodifacoum to birds in a native ecosystem.

Research and conservation priorities

Current management practice in New Zealand views ecological costs of using toxins, where pest mammals are present, as much lower than damage costs if they are not used (Innes & Barker 1999). However, information about sustained toxin use and its flow through a native food web is lacking. As a precautionary approach, DoC has adopted a policy to reduce the use of brodifacoum and other anticoagulant poisons in the conservation estate. However, it is used in a sustained manner by DoC in island protection, by Regional Councils to control mammalian pests at key ecological sites and by the Animal Health Board and Regional Councils over vast tracts of the country in Tb vector control.

In native systems where anticoagulant poison is used to detect rodent invasions, toxins may be distributed via native vectors. The consequences of sustained poison use for non-target wildlife in these systems are unknown. Recent field evidence suggests that reptiles and other primary consumers may take toxic baits where it is used repeatedly (Appendix 3). One approach to investigate poison distribution in these systems is to test for brodifacoum residues in carcasses of a variety of native fauna collected opportunistically from an island. Toxicological and stomach contents analyses from a variety of fauna could be used to infer toxin pathways and information on the accumulation of toxin in higher-trophic level species. However, we question whether toxic baits are the best tool to use in island protection.

Present island protection measures involve rodenticide bait stations, which have not been trialled for effectiveness and were not designed for their current use (O'Connor & Eason 2000, Dilks & Towns 2002, Roberts 2003). Lack of detection of experimentally released (Russell *et al.* 2005) and accidentally introduced (Thorsen *et al.* 2000) rodents onto offshore islands confirm fears that traditional methods may fail to detect invading rodents on mammal-free islands where there is a natural abundance of food (Dilks & Towns 2002). Successful use of brodifacoum as a rodenticide where rodents are present in an ecosystem does not necessarily translate to effectiveness at attracting rats which arrive on an island with an abundance of seeds, fruit and invertebrates (Dilks & Towns 2002).

We recommend that managers consider alternatives to anticoagulant poison use in rodent detection on mammal-free islands. Bait stations are designed to provide an early

warning of introduced mammals, as well as having the potential to kill an invading rodent in a single dose. Early warning could equally be performed by a non-toxic method of identifying the presence of mammals, such as tracking tunnels, wax tags or electronic detection (see Dilks & Towns 2002 for a description of these methods). Such use of non-toxic methods should be backed up by a contingency plan, i.e., a preestablished standard procedure of trapping and monitoring to be implemented following rodent detection (see Roberts, 2003).

Conclusion

Most knowledge of non-target effects of brodifacoum use are derived from postbaiting monitoring of one-off island eradication operations. The risk of secondary exposure to native non-targets is likely to be greater when brodifacoum is applied to the environment in a sustained manner. In New Zealand, brodifacoum is widely used in continuous mammal-control operations and in island protection. Protecting the mammal-free status of offshore islands with brodifacoum, involves continuous supply of anticoagulant poison to systems in which a more representative suite of native fauna interact, than that found in sympatry with introduced mammals on the mainland. In these systems, taxa which have not been the focus of research into effects of brodifacoum poisoning to date are often abundant and fulfil important ecosystem roles. Native invertebrates and reptiles consuming brodifacoum may pose a significant risk of secondary poisoning to birds, exacerbated by its sustained use and the process of bioaccumulation. As a precautionary approach, we recommend reducing the sustained use of brodifacoum baits in mammal-free locations by implementing non-toxic methods of rodent detection. However, where sustained brodifacoum use is required, research priority must be given to investigating the roles of all potentially significant native consumers as vectors of the toxin.

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APPENDIX 3

Consumption of the anticoagulant poison brodifacoum by New Zealand common geckos, *Hoplodactylus maculatus*¹

Anticoagulant poisons, particularly the second-generation anticoagulant brodifacoum, are used extensively both to eradicate pest mammals from offshore islands and to detect reinvasions (e.g., Dilks & Towns 2002). Conservation benefits of pest mammal eradication usually outweigh the costs of temporary population die-back of non-target natives (Innes & Barker 1999). Considerable research documents brodifacoum poisoning of native bird species (reviewed by Eason et al. 2002) and invertebrates (e.g., Spurr & Drew 1999) following mammalian pest eradication. However, research on other taxa (e.g., reptiles) and on ecosystem-level effects of chronic brodifacoum use is sparse. Brodifacoum is a potent and persistent rodenticide, lasting for at least 6 months in organs and tissue, which exacerbates the risk of secondary poisoning of non-target species (e.g., Eason *et al.* 2002).

Potential risk of brodifacoum poisoning to reptiles is thought to be low, as reptiles have a blood coagulation chemistry distinct from that of mammals (Merton 1987). However, few studies have investigated anticoagulant bait consumption by reptiles in the wild (but see Merton 1987 and Thorsen *et al.* 2000).

Mana Island, Cook Strait, New Zealand (41°40'S, 174°00'E) underwent eradication of mammals in 1991 and has since been the focus of an intensive ecological restoration program. To protect Mana Island from mammal reinvasion, 42 wooden

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boxes baited with brodifacoum poison (Pestoff®; 20 ppm; which has a half-life of 157 days in soil) and peanut-oil flavoured wax tags are deployed along the shoreline, and rebaited regularly (every 4-6 weeks). Common geckos, *Hoplodactylus maculatus*, regularly use the bait boxes as refugia (Hare & Hoare 2005).

In May 2004, we surveyed *H. maculatus* from 14 bait boxes. Handling induced defecation by 16% (12 of 74) of geckos. We observed 3 adult (one male and two females; 69-81 mm SVL) geckos (25%) deposit bright blue-green faecal material, in contrast to normal, dark-brown faeces. One other adult (73 mm SVL) male gecko exhibited blue/green spots inside the throat and abdominal skin. Blue-green faecal material deposited was the same colour as the dyed brodifacoum bait within the boxes, which led us to infer consumption of the toxin by these geckos (based on Freeman et al. 1996). One of the 3 geckos that defecated bait was in the late stages of pregnancy with two embryos (as determined by palpation), which raises the question of whether anticoagulant poison may detrimentally affect offspring. Other than these obvious signs that geckos consume toxic bait, all appeared to be in good condition (body condition, defined as $\log(mass)/\log(SVL)$, was 0.557 ± 0.086 , and did not differ significantly from body condition of adult geckos that did not show signs of bait consumption $0.536 \pm$ 0.079; $F_1 = 0.4946$, P = 0.4839), had few ectoparasites and no sores or open wounds. Only one gecko was found dead during the survey, a desiccated juvenile, with no evidence of brodifacoum consumption.

Our observation of bait consumption by *H. maculatus* in nature is the first to document both brodifacoum consumption by geckos and consumption of a toxin by reptiles when it is continuously provided. Only two published studies report reptile consumption of brodifacoum bait in the wild. Following pest mammal eradication on Round Island, Mauritius, Telfair's skink, *Leiolopisma telfairi*, suffered mortality from consuming brodifacoum bait (Merton 1987), and Wright's skink, *Mabuya wrightii*, from Frégate Island, Seychelles, also consumed brodifacoum bait, though effects on these skinks were not studied (Thorsen *et al.* 2000).

Formulating management strategies to mitigate the potential effects of anticoagulants and other toxins on lizards is hampered by a lack of information (Spurr 1993). Published lethal dose (LD₅₀) data on acute toxicity of anticoagulants to reptiles do not exist. However, LD₅₀ data for lizards exposed to sodium monofluoroacetate (1080) suggest that poisons are unlikely to induce mortality in lizards, as lethality would require vast quantities of toxin to be consumed (e.g., McIlroy *et al.* 1985). The hypothesis that anticoagulant poisons are unlikely to pose lethal threats to reptiles is supported by a laboratory study of anticoagulant consumption by McCann's skinks, *Oligosoma maccanni*. Skinks which consumed toxic pindone (a first-generation anticoagulant) bait (97%), showed no adverse short-term effects (Freeman *et al.* 1996). However, potential sub-lethal effects of anticoagulants include interference with reptiles' abilities to thermoregulate, which may prove fatal under conditions of environmental stress (Merton 1987).

Traditionally, discussions concerning the risk of secondary poisoning to non-target native species have focussed on target (i.e., mammalian) prey species as vectors for anticoagulant transportation (e.g., Eason & Wickstrom 2001). Our finding extends concerns for non-target species, as brodifacoum consumption by reptiles poses a risk of secondary poisoning, particularly to native avian predators of lizards. Brodifacoum is a highly potent and persistent anticoagulant; ecosystem-level research is required if continued use of brodifacoum is deemed an appropriate management option to detect rodent invasions.

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