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Does evolution in isolation from mammalian predators have behavioural and chemosensory consequences for New Zealand lizards?

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Abstract: Recently introduced mammalian predators have had devastating consequences for biotas of archipelagos that were isolated from mammals over evolutionary time. However, understanding 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 on native lizard populations of the relatively recent and patchy history of mammalian introductions to New Zealand's islands provide an opportunity to examine the consequences of relaxed selection. We 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 up to 16 million years; some now co-occur with mammals, while others remain in mammal-free locations. A skink species that evolved with mammals and has recently been introduced to New Zealand is included for comparison. Lizard behavioural patterns were correlated with recent and historical experience of mammals. Lizards always isolated from mammals exhibited the most antipredator freeze behaviour, whereas one that coevolved with mammals exhibited greatest activity (movements). However, predator chemical cues did not induce specific antipredator responses in any species indicating that these behavioural patterns are not linked to chemosensory predator detection alone.

Keywords: antipredator behaviour, chemical cues, chemoreception, gecko, olfaction, predation, rat, relaxed selection, reptile, skink

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; Epp & Gabor 2008; Gall & Mathis 2010; Sih et al. 2010). 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 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 arbitrarily transported provide a powerful context to test questions concerning the consequences of isolation from a predator guild. Lizards in New Zealand with varying histories of exposure to predatory mammals provide

an opportunity to test the roles of coevolution and recent experience with a mammalian predator guild 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 up to 16 million years, prior to human contact c. 800 years BP (Wilmshurst et al. 2008). Islands never reached by mammals or from which mammals are removed often support high lizard diversity and abundance (e.g. Daugherty et al. 1990; Towns 1996; Hoare et al. 2007b). 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 been so susceptible to invasive mammals (Gibbons et al. 2000).

New Zealand lizards coevolved with primarily visual

native predatory birds, other lizards and tuatara (*Sphenodon punctatus*) as predators (Meyer-Rochow 1988; Meyer-Rochow & Teh 1991; Worthy & Holdaway 2002). The visual crypsis and secretive behaviours exhibited by native lizards (e.g. Hare et al. 2007) are presumably the results of strong selective pressure to avoid detection by native predators. However, this strategy may be unsuitable for the 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), reflecting a broader lack of olfactory studies available to inform conservation (Campbell-Palmer & Rosell 2011). Endemic diurnal geckos, *Naultinus manukanus*, show some ability to detect strong (faecal) cues of native reptilian predators (tuatara) as well as conspecifics and food (Hoare et al. 2007a), suggesting that New Zealand lizards can use chemosignals for a range of purposes, possibly including their antipredator behaviour. 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, e.g. weka *Gallirallus australis*), selection on chemosensory abilities of New Zealand lizards may have been relaxed, resulting in their loss. Geckos are thought to have colonised New Zealand 40.2–24.4 million years ago from Australia and skinks ~18.3 million years ago from New Caledonia via overwater dispersal and island hopping (Chapple et al. 2009; Nielsen et al. 2011; Chapple & Hitchmough 2016). Thus, both groups have been isolated from mammalian predators for several millennia.

Groups of lizards in New Zealand provide an opportunity to investigate both behavioural and chemosensory consequences of evolution without selective pressure from mammalian predators as: (1) native geckos and skinks evolved in isolation from mammalian predators; and (2) an introduced skink (plague or rainbow skink *Lampropholis delicata*) coevolved with mammals in Australia.

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*, and kurī, *Canis familiaris*, have been present on mainland New Zealand for ~800 years (Wilmshurst et al. 2008), and another 30 species of mammals introduced by European settlers have established in the past c. 200 years (King 2005), though a number of offshore islands remain mammal-free.

We investigate the ability of lizards to recognise chemicals of predatory tuatara, a reptile endemic to New Zealand, and ship rats, *R. rattus*, which established in the North Island after 1860 (King 2005). The scope of this study is limited to odour-related behaviour. We test whether experience of, and evolution with, mammalian predators determines behavioural patterns and chemosensory predator recognition abilities of lizard prey by addressing the following questions.

(1) Do predator detection abilities vary among species isolated from mammalian predators? We compare four lizard species on a mammal-free offshore island. The species encompassed skinks and geckos, including species that are rare or common at locations where they now coexist with mammals.

(2) Do behaviours and predator detection abilities vary across populations of the same species according to recent exposure to mammalian predators? We 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? We compare native skinks that were evolutionarily isolated from mammalian predators with an introduced skink that coevolved with mammals and snakes.

Methods

Study sites

The 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; maximum distance between sites 100 km). The North Island sites are inhabited by a diverse range of introduced mammals, including rodents, mustelids and cats (*Felis catus*) (King 2005). Mammals never reached North Brother Island. Cats were introduced to Stephens Island in the late 19th century and spread quickly, but lighthouse keepers eradicated them by 1925 (Brown 2000) and the island has remained free of predatory mammals since then. Introduced plague skinks, which coevolved with mammalian predators as well as birds and reptiles, were collected from the Otara and Mount Wellington suburbs in Auckland, North Island (Fig. 1). Rainbow skinks 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 much of the North Island, although have only recently reached the Marlborough region of the South Island where eradication attempts are underway (Tingley et al. 2016; R. Hitchmough, Department of Conservation, pers. comm.).

Under a pre-human predation regime, predators of native New Zealand lizards were predominantly birds, especially kingfishers (*Halcyon sancta*), owls, gulls, rails, harriers, adzebills 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 were 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. In the absence of data, we assume that the intensity of bird predation is approximately equivalent at both mammal-affected and mammal-free sites (because the prevalence of introduced birds offsets loss of native bird abundance caused by mammalian predation).

Study species

Behaviours of the widespread and abundant common skinks, *Oligosoma polychroma* (Chapple et al. 2009), and Raukawa geckos, *Woodworthia maculata*, 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 both speckled skinks and Marlborough green geckos as 'Declining' due to human
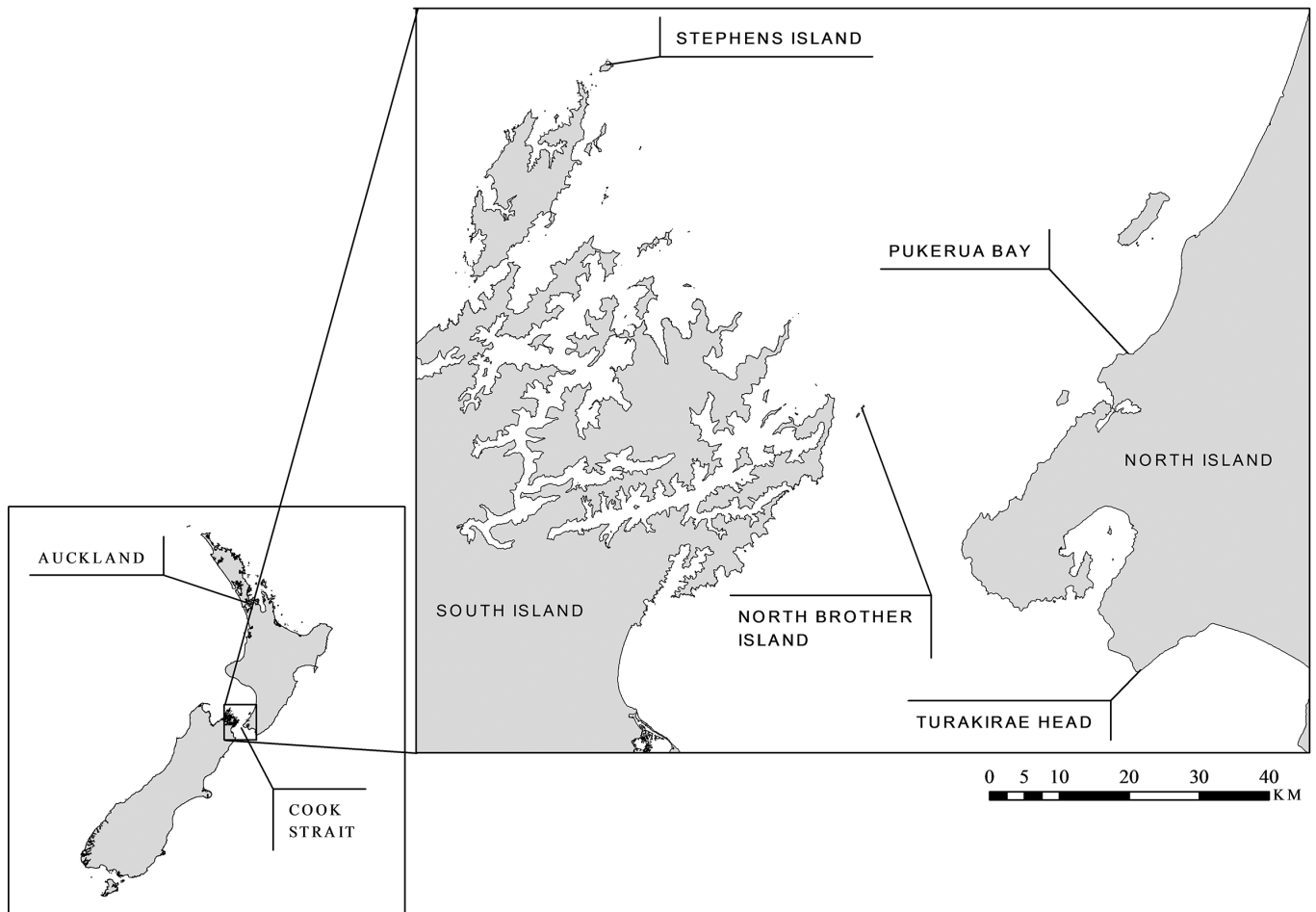
Figure 1. Sampling localities for lizards. Raukawa geckos, *Woodworthia maculata*, and common skinks, *Oligosoma polychroma*, were collected from all sites marked in the Cook Strait region. The rare Marlborough green geckos, *Naultinus manukanus*, and speckled skinks, *O. infrapunctatum*, were collected from Stephens Island. Introduced plague 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.

activities (Hitchmough et al. 2016). Common skinks and Raukawa 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 plague skinks were used as an out-group that coevolved with mammals and compared with common skinks. Plague skinks can use chemosensory cues to respond to snake predators in their native range (Downes & Hoefer 2004).

All skinks and geckos used in this study were captured through pitfall trapping or hand searching. Raukawa geckos and common skinks were captured 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 plague 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 >30 g) were measured. Lizards captured on Stephens and North Brother Islands were held temporarily in captivity (in temporary laboratories inside buildings) on the respective islands for behavioural trials. Those from mainland sites were transported by vehicle in cotton bags inside a cool, ventilated container to either the Victoria University of Wellington (VUW; lizards from Pukerua Bay and Turakirae Head) or the Albany campus of Massey University (MU; plague skinks from Auckland) for behavioural trials.

All lizards were kept individually in 2 L plastic containers with 1 × 1 mm wire mesh (165 × 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°C to 26.3°C) conditions; at VUW temperature of the room ranged from 13.6°C 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°C to 23.2°C) conditions. We minimised the time lizards were held in captivity for this research as much as possible (range 7 to 19 d) and returned them to the wild at their exact point of capture.

Table 1. Capture information for native geckos *Woodworthia maculata* (Wm) and *Naultinus manukanus* (Nm), and skinks *Oligosoma polychroma* (Op) 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 >30 g and to 0.1 g for lizards <30 g.

Species	Abundance	Site	Predation regime	n	♂	♀ (PG)[a]	Capture dates	SVL (mm)	Mass (g)
Wm	common	Stephens Is.	Natural	30	13	17 (13)	3–16 Nov. 2003	55–75	3.5–10.5
Wm	common	North Brother Is.	Natural	30	12	18 (6)	23–29 Feb. 2004	65–80	7.0–12.0
Wm	common	Pukerua Bay	Modified	29[b]	12	17 (0)	3 Feb. – 23 Apr. 2004	63–75	5.0–9.5
Wm	common	Turakirae Head	Modified	30	19	11 (0)	17 Apr. 2005	52–66	2.5–7.5
Op	common	Stephens Is.	Natural	9	6	3 (1)	10–20 Nov. 2003	50–66	2.0–5.1
Op	common	North Brother Is.	Natural	30	10	20 (0)	24–27 Feb. 2004	55–68	2.5–5.0
Op	common	Pukerua Bay	Modified	30	17	13 (0)	2 Feb. – 17 Mar. 2004	53–65	2.3–4.5
Op	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

[a]P = pregnant, G = gravid; [b]10 of 29 *W. maculata* at Pukerua Bay were trialled at night, during their activity phase (see methods).

Experimental procedure

Chemical cues can mediate interactions including antipredator behaviours in a range of reptiles, including lizards (Van Damme & Quick 2001), with the natural pheromones involved identified and validated with behavioural tests (reviewed by Houck 2009; Mason & Parker 2010). Our experimental methodology for testing prey responsiveness to predator chemical cues is adapted from Downes and Shine (1998), and has successfully evoked antipredator responses in Australian and native New Zealand geckos (Downes & Shine 1998; Hoare et al. 2007a). The experimental methodology follows the same procedures used for adult *N. manukanus* described in Hoare et al. (2007b); brief methods and differences are explained here. The experimental arena was a clear plastic enclosure (280 × 250 × 210 mm, L × W × H) containing a plain cotton cloth of the same dimensions as the base of the enclosure and covered with the scent to be tested. After being thoroughly washed, this cloth was treated in one of four ways (Hoare et al. 2007a): (1) negative control, no scent; (2) positive (chemical pungency) control, cloth was sprayed with commercial cologne ('Smiley') and air-dried; (3) tuatara scent, cloth was sprayed with a solution of tuatara urine and faeces; and (4) rat scent, cloth was sprayed with a solution of ship rat urine and faeces. The same dose was applied to each cloth by depressing the trigger of the bottle containing predator scent or cologne the same number of times to avoid any dose-dependent effects.

Predator odours derived from urine or faeces have frequently been used in studies of predator recognition. Although a small number of recent studies suggest that skin and fur-derived predator odours may have a more profound lasting effect on prey species than urine or faeces (Apfelbach et al. 2005), we were restricted to using urine and faeces due to availability and consistency across both taxonomic groups of predators. Samples were collected from both captive (at VUW) and wild-caught (from Stephens and North Brother Islands) tuatara and captive rats (from Ngā Manu Nature Reserve, Waikanae). Ship rats are known predators of Raukawa geckos (Hoare et al. 2007c), and likely predators of other New Zealand lizards. A recent 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 us to take a cautious approach to feeding the predators whose urine and faeces were used as the chemical cues in experiments of lizard responsiveness. We fed captive tuatara and rats diets of invertebrates and/or grains, and never lizards. Wild-caught tuatara may have consumed lizards; gecko and skink remains are found in c. 3% of tuatara scats on Stephens Island (Walls 1981). Tuatara were caught by hand, transported to laboratory facilities (at VUW and on islands) in cotton catching bags and housed overnight in a ventilated enclosure (800 × 400 × 400 mm, L × W × H) with water. Faecal and urine samples were passively collected the next morning and tuatara released either in the captive facility (VUW) or at their point of capture (islands). Rats were not captured, but their urine and faeces were collected from the enclosure in which they are held at Ngā Manu Nature Reserve.

All behavioural trials were conducted during daylight hours except for 10 Raukawa geckos, which were tested at night. Geckos in the genus *Woodworthia* are diurno-nocturnal, exhibiting extensive indirect basking during the day as well as being active at night (Gibson et al. 2015) and show no strong pattern in metabolic rate over a 24-hour period (Hare et al. 2006). Testing a subset of geckos at night enabled us to evaluate any behavioural differences associated with time of day.

Behaviour of lizards was observed continuously for 8 minute (duration determined based on pilot study; see Hoare et al. 2007a) periods using an observational data logging programme that we 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 include running, remaining motionless, vibrating the tail laterally against the substrate, defecating and/or vocalising (Daniels et al. 1986). In contrast, we expect normal maintenance behaviour of lizards to include a greater proportion of slow, stalking walk behaviour and snout licking. Therefore, we chose to measure a variety of behavioural actions that represent both antipredator defences and normal maintenance behaviours, but acknowledge that a full spectrum of antipredator responses could not be measured (e.g. apprehension). The relative proportions of these behaviours were used to indicate responsiveness to chemical stimuli. Either the duration (in s; 1 to 10) or the frequency (11 and 12) of the following spatial use, behavioural and locomotor acts was recorded.

(1) 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 (to spatially avoid the predator), including running, walking, climbing or nudging the wall. We 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 Hoare et al. 2007a) 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* (Hoare et al. 2007a). 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 plague 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.

Statistical analyses

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

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 Raukawa 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) Raukawa geckos from Pukerua Bay, 10 of which were trialled during the night 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 examine univariate effects where MANOVAs were significant.

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.

Species-specific linear mixed effects (LME) models were then used to examine univariate differences in behaviour. 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.

Interspecific comparisons

We compared the responses of rare vs 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 plague 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 plague skinks; these included significant factors from the MANOVA.

Results

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 (data presented are for common species and 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);
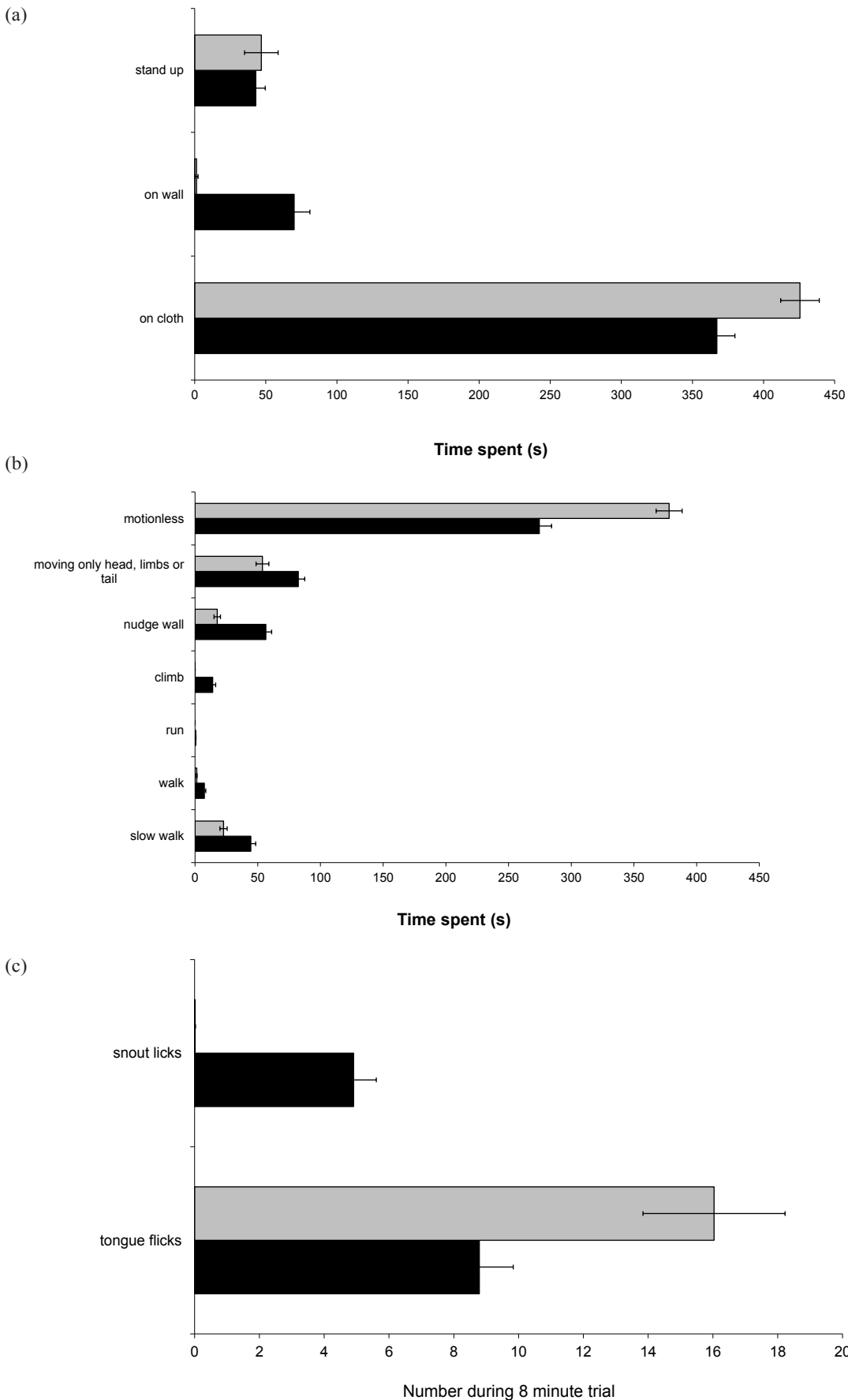
(a)

(b)

(c)

Figure 2. (a) Position in the test arena, (b) activities and (c) actions of Raukawa geckos, *Woodworthia maculata* (black bars) and common skinks, *Oligosoma polychroma* (grey bars) during negative control trials (8 min in duration), averaged across individuals from all sites. Error bars are standard errors.

therefore, significant variation in these activities was 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).

Reproductive condition of female lizards did not alter their overall behaviour ($F_{10,120} = 1.261$, $P = 0.256$) or response to scent stimuli ($F_{30,352.9} = 1.269$, $P = 0.266$). Therefore, we pooled pregnant and non-pregnant female lizards in further tests. Time of trial (day-night) influenced behaviour of the primarily nocturnal Raukawa 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 ($F_{30,191.46} = 0.647$, $P = 0.921$).

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

Under a natural predation regime, on mammal-free Stephens Island, we 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).

Therefore, the results presented hereafter pertain to common skinks and Raukawa geckos, unless otherwise stated.

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

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 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 ($F_{10,518} = 2.194$, $P = 0.002$), 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.

Site-specific differences in skink behaviours (Table 3) 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. Conversely, skinks from locations in which

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 million years). Widespread and abundant endemic geckos, *Woodworthia maculata*, and skinks, *Oligosoma 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.	We presented individual *W. maculata* and *O. polychroma* 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 the mammals influences lizard behaviours.	We compared behaviours of *W. maculata* and *O. polychroma* collected from two mammal-affected sites and two mammal-free sites.	Behaviours of geckos and skinks were correlated with presence of mammals (MANOVA: $P < 0.0001$ for both). Exposure to mammals induced greater activity and less antipredator freeze behaviour (Figs. 3 & 4).
C. Lizards exposed to mammals show a greater response to predator chemical cues.	We compared responses of *W. maculata* (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.	We compared responses of rare *N. manukanus* vs. common *W. maculata* and rare *O. infrapunctatum* vs. common *O. polychroma* 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.	We compared responses of introduced *L. delicata* vs. native *O. polychroma* 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 among lizards.	We compared behaviours of introduced *L. delicata* vs. native *O. polychroma*.	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).

Table 3. Results of model selection to determine the most significant predictors of lizard behaviour. '*' represents an interaction term.

Behavioural act	*Woodworthia maculata* Predictor(s)	F value	df	P	*Oligosoma polychroma* Predictor(s)	F value	df	P
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				

[a]These results must be treated with caution, as the behaviours were rarely performed (Fig. 2).
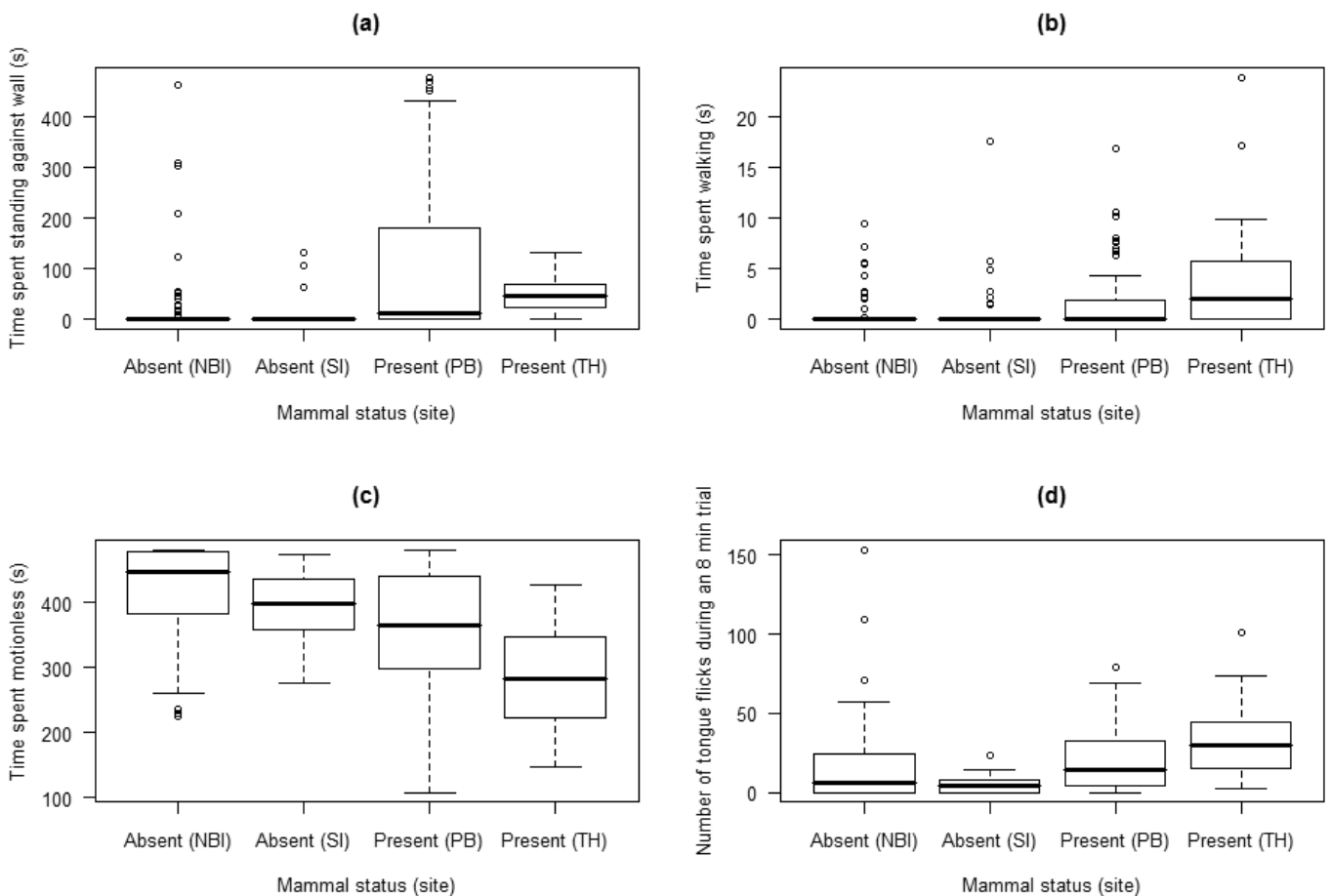

Figure 3. Behavioural actions of common skinks, *Oligosoma polychroma*, during all scent trials (pooled) at each site. Behavioural actions portrayed are time spent: (a) standing against wall, (b) walking, and (c) motionless, and (d) lingual sampling of the substrate. Significant differences between populations 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 3). Boxplots include the median (thick black line), first and third quartiles (upper and lower sides of the box), 1.5 * interquartile range (whiskers) and outliers (circles beyond the whiskers).

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 ($t_{309} = -2.024$, $P = 0.044$).

Our finding that the scent stimuli presented to geckos influenced their positions within enclosures (Table 3) was driven primarily by cologne (the positive control) inducing geckos to spend more time on the enclosure walls (climbing) and less on the scent cloth than either a negative control or predator chemical cues (Fig. 4b). Tuatara (native predator) chemical cues produced a similar, yet weaker, response. Scent-induced 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 where 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.

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

Introduced plague skinks, which co-evolved with mammals, differed from native common skinks in their behavioural responses to scent stimuli ($F_{16,372} = 2.952$, $P < 0.001$). These differences were attributable to plague 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, plague skinks were more active than common skinks across a range of activities in trials, and their lingual sampling of the substrate was more frequent (Table 2; Fig. 5).

Discussion

Chemoreceptive abilities of New Zealand lizards

We find little evidence to suggest that New Zealand lizards detect and respond to native or introduced predators using
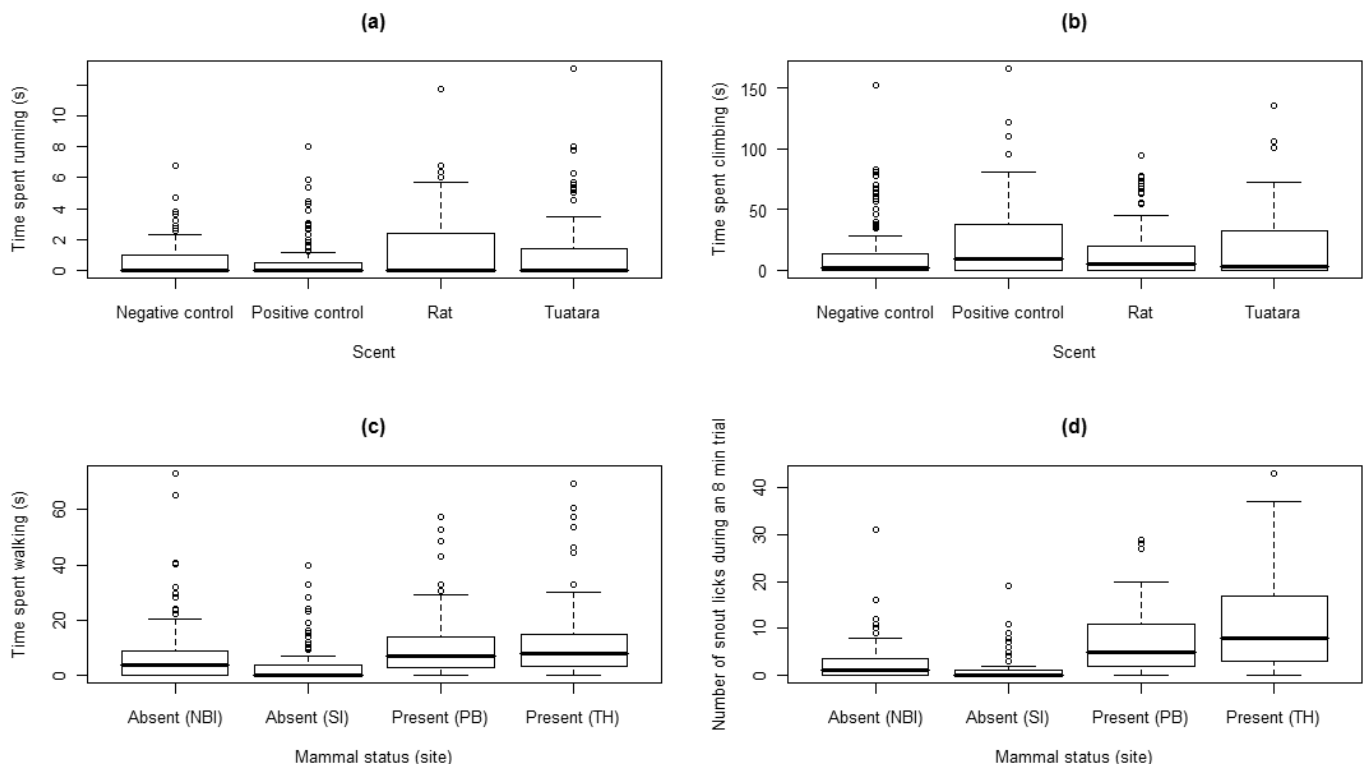

Figure 4. Behavioural actions of Raukawa geckos, *Woodworthia maculata*, in response to scent stimuli (a & b), and in relation to sites from which geckos were sourced (c & d). Behavioural actions portrayed are time spent: (a) running, (b) climbing, and (c) walking, and (d) licking snout. Site abbreviations are: 'NBI' = North Brother Island, 'SI' = Stephens Island, 'PB' = Pukerua Bay, and 'TH' = Turakirae Head. Boxplots include the median (thick black line), first and third quartiles (upper and lower sides of the box), 1.5 * interquartile range (whiskers) and outliers (circles beyond the whiskers).
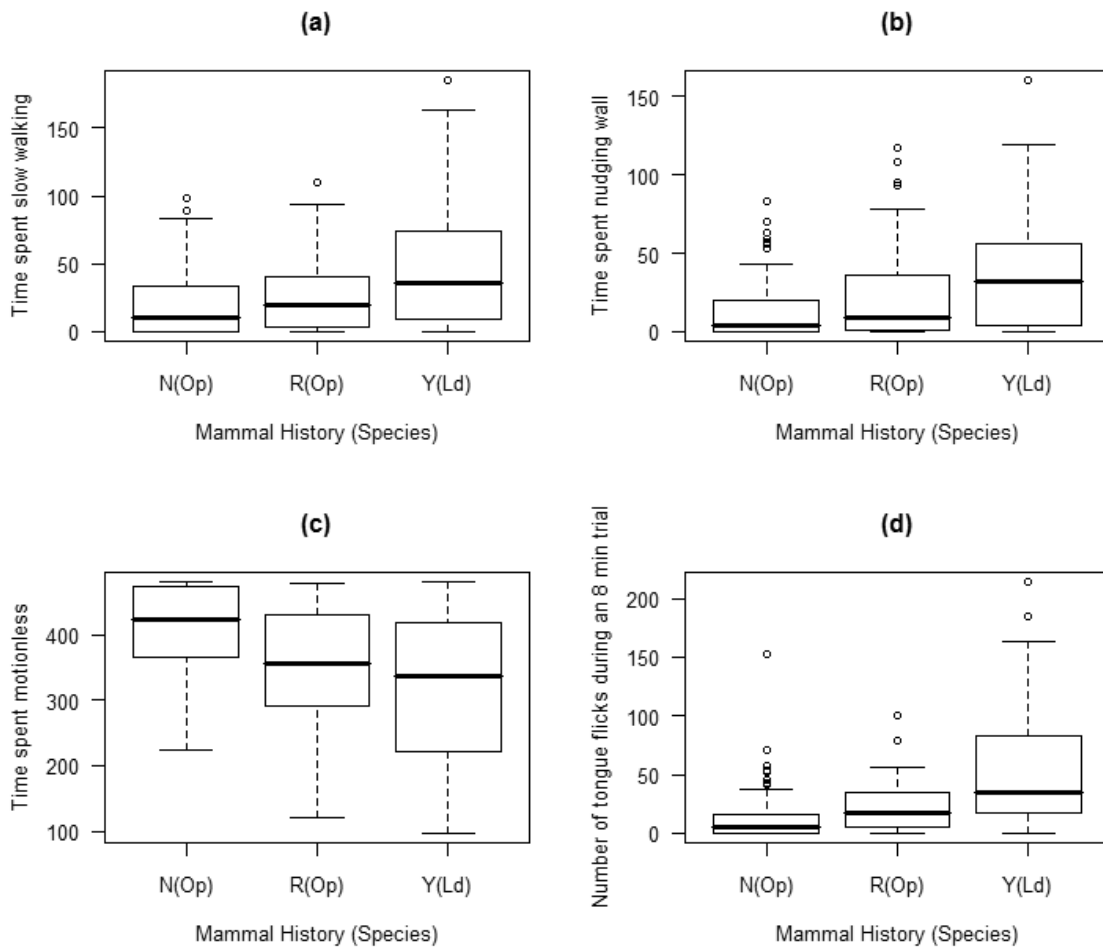
Figure 5. Behavioural variation among native common skinks, *Oligosoma polychroma* (Op) and introduced plague skinks, *Lampropholis delicata* (Ld) according to history of evolution with introduced mammalian predators. Plague skinks co-evolved with mammals (Y), while some common skink populations do not 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. Boxplots include the median (thick black line), first and third quartiles (upper and lower sides of the box), 1.5 * interquartile range (whiskers) and outliers (circles beyond the whiskers).

chemical cues from urine or faeces alone. We acknowledge that multiple predator stimuli including direct cues (e.g. visual, auditory) that indicate imminent predation risk may be needed to elicit a full antipredator response. However, ectotherms in a cool temperate climate are severely limited by environmental temperature in their ability to escape from a predator. As such, New Zealand lizards could reasonably be expected to respond to indirect cues alone, as has been demonstrated for other lizards (Downes & Shine 1998; Downes & Adams 2001).

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. Dumont (2015) found that common skinks and glossy brown skinks (*O. zelandicum*) showed similarly little avoidance behaviour in response to experimental presentation of the scent of other predatory mammals (ship rats or hedgehogs *Erinaceus europaeus*).

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). Our 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 (i.e. native predators (birds, tuatara and larger lizards) are primarily visual predators; Meyer-Rochow 1988; Meyer-Rochow & Teh 1991; Worthy & Holdaway 2002).

Chemoreception alone does not appear to mediate detection or avoidance of mammalian predators of New Zealand lizards, irrespective of coevolution or experience of this predatory threat (this study; Dumont 2015). Despite prey avoidance of predator chemical cues being demonstrated across a wide range of taxa, 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. 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).

There are two main reasons for the differences in snake and lizard antipredator responses to mammalian scent: (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.

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

Although the behavioural patterns of New Zealand lizards do not appear to be mediated by chemoreception alone, they are highly correlated with the predator regimes to which they are exposed. The presence or absence of mammals from a site had far greater explanatory power for behavioural differences than did environmental factors, as evidenced by the statistical modelling. Recent coexistence with predatory mammals seems to have induced a shift among lizards from antipredator freeze behaviour towards greater activity. The trend was exemplified by a behavioural comparison between common and plague 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 (Hoare et al. 2007b) support this lab-based evidence. Our 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. Hare et al. 2007) 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 adaptation of some prey species to novel selective pressures (reviewed by Strauss et al. 2006). For example, predatory cats 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.

Conclusion

Investigation of the consequences of evolution in isolation from mammals has revealed that behaviours of lizards exposed to predation pressure from introduced mammals differ markedly from those under a natural (bird- and reptile-dominated) predation regime. However, predator chemical cues do not appear to induce specific antipredator responses in lizards, indicating that these behavioural patterns are not linked to chemosensory predator detection alone. Our findings support field evidence that lizards that evolved in isolation from mammalian predators use spatial avoidance behaviour to persist in sympatry with these novel predators (Hoare et al. 2007b), but the mechanisms through which they detect introduced mammals are yet to be discovered.

Acknowledgements

References

Akaike H 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F eds. Second International Symposium on Information Theory. Budapest, Akademiai Kiado. Pp. 267–281.

Amo L, Lopez P, Martin A 2004. Chemosensory recognition and behavioral responses of wall lizards, *Podarcis muralis*, to scents of snakes that pose different risks of predation. Copeia 2004: 691–696.

Apfelbach R, Blanchard CD, Blanchard RJ, Hayes RA, McGregor IS 2005. The effects of predator odors in mammalian prey species: a review of field and laboratory studies. Neuroscience & Biobehavioral Reviews 29: 1123–1144.

Armsworth CG, Bohan DA, Powers SJ, Glen DM, Symondson WOC 2005. Behavioural responses by slugs to chemicals from a generalist predator. Animal Behaviour 69: 805–811.

Blumstein DT 2002. Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. Journal of Biogeography 29: 685–692.

Blumstein DT, Daniel JC 2005. The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society of London – Series B. Biological Sciences 272: 1663–1668.

Blumstein DT, Mari M, Daniel JC, Ardron JG, Griffin AS, Evans CS 2002. Olfactory predator recognition: wallabies may have to learn to be wary. Animal Conservation 5: 87–93.

Brown D 2000. Stephens Island: ark of the light. Blenheim, Blenheim Print. 248 p.

Bunin JS, Jamieson IG 1996. Responses to a model predator of

New Zealand's endangered takahe and its closest relative, the pukeko. Conservation Biology 10: 1463–1466.

Burghardt GM 1970. Chemical perception in reptiles. In: Johnston JW, Moulton DG, Turk A eds. Advances in chemoreception. New York, Appleton-Century-Crofts. Pp. 241–308.

Burnham KP, Anderson DR 1998. Model selection and inference: a practical information-theoretic approach. New York, Springer-Verlag. 355 p.

Campbell-Palmer R, Rosell F 2011. The importance of chemical communication studies to mammalian conservation biology: a review. Biological Conservation 144: 1919–1930.

Case TJ, Bolger DT 1991. The role of introduced species in shaping the distribution and abundance of island reptiles. Evolutionary Ecology 5: 272–290.

Cassels R 1984. The role of prehistoric man in the faunal extinctions of New Zealand and other Pacific islands. In: Martin PS, Klein RG eds. Quaternary extinctions - a prehistoric revolution. Tucson, The University of Arizona Press. Pp. 741–767.

Chapple DG, Hitchmough RA 2016. Biogeography of New Zealand lizards. In: Chapple DG ed. New Zealand lizards. Switzerland, Springer. Pp. 109–131.

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

Chiszar D, Lukas W, Smith HM 1997. Response to rodent saliva by two species of rodentiophagous snakes. Journal of Chemical Ecology 23: 829–836.

Clark RW 2004. Timber rattlesnakes (Crotalus horridus) use chemical cues to select ambush sites. Journal of Chemical Ecology 30: 607–617.

Cooper WE, Burghardt GM 1990. Vomerolfaction and vomodor. Journal of Chemical Ecology 16: 103–105.

Coss RG 1999. Effects of relaxed natural selection on the evolution of behavior. In: Foster SA, Endler JA eds. Geographic variation in behavior: perspectives on evolutionary mechanisms. Oxford, Oxford University Press. Pp. 180–208.

Cowles RB 1938. Unusual defense postures assumed by rattlesnakes. Copeia 1938: 13–16.

Daniels CB, Flaherty SP, Simbotwe MP 1986. Tail size and effectiveness of autotomy in a lizard. Journal of Herpetology 20: 93–96.

Daugherty CH, Towns DR, Atkinson IAE, Gibbs GW 1990. The significance of the biological resources of New Zealand islands for ecological restoration. In: Towns DR, Daugherty CH, Atkinson IAE eds. Ecological restoration of the New Zealand islands. Wellington, New Zealand Department of Conservation. Pp. 9–21.

Downes SJ, Adams M 2001. Geographic variation in antisnake tactics: the evolution of scent-mediated behavior in a lizard. Evolution 55: 605–615.

Downes SJ, Bauwens D 2002. Does reproductive state affect a lizard's behavior toward predator chemical cues? Behavioral Ecology and Sociobiology 52: 444–450.

Downes SJ, Hoefer AM 2004. Antipredatory behaviour in lizards: interactions between group size and predation risk. Animal Behaviour 67: 485–492.

Downes SJ, Shine R 1998. Sedentary snakes and gullible geckos: predator-prey coevolution in nocturnal rock-dwelling reptiles. Animal Behaviour 55: 1373–1385.

Dumont CT 2015. An investigation into declining skink

populations and their behavioural responses to introduced mammalian predators. 145 p.

Epp KJ, Gabor CR 2008. Innate and learned predator recognition mediated by chemical signals in Eurycea nana. Ethology 114: 607–615.

Gall BG, Mathis A 2010. Innate predator recognition and the problem of introduced trout. Ethology 116: 47–58.

Gibbons JW, Scott DE, Ryan TJ, Buhlmann KA, Tuberville TD, Metts BS, Greene JL, Mills T, Deiden Y, Poppy S, Winne CT 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50: 653–666.

Gibson S, Penniket S, Cree A 2015. Are viviparous lizards from cool climates ever exclusively nocturnal? Evidence for extensive basking in a New Zealand gecko. Biological Journal of the Linnean Society 115: 882–895.

Gill BJ, Whitaker AH 1996. New Zealand frogs and reptiles. Auckland, David Bateman Limited. 112 p.

Hare KM 2005. The paradox of nocturnal lizards. Unpublished PhD thesis. Victoria University of Wellington. 149 p.

Hare KM, Pledger S, Thompson MB, Miller JH, Daugherty CH 2004. Conditioning reduces metabolic rate and time to steady-state in the lizard Naultinus manukanus (Reptilia: Gekkonidae). Comparative Biochemistry and Physiology Part A 139: 245–250.

Hare KM, Pledger S, Thompson MB, Miller JH, Daugherty CH 2006. Daily patterns of metabolic rate among New Zealand lizards (Reptilia: Lacertilia: Diplodactylidae & Scincidae). Physiological and Biochemical Zoology 79: 745–753.

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

Head ML, Keogh JS, Doughty P 2002. Experimental evidence of an age-specific shift in chemical detection of predators in a lizard. Journal of Chemical Ecology 28: 541–554.

Hitchmough R, Barr B, Lettink M, Monks J, Reardon J, Tocher M, van Winkel D, Rolfe J 2016. Conservation status of New Zealand reptiles, 2015. 14 p.

Hoare JM, Pledger S, Nelson NJ 2007a. Chemical discrimination of food, conspecifics and predators by apparently visually-oriented diurnal geckos, Naultinus manukanus. Herpetologica 63: 184–192.

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

Hoare JM, Adams LK, Bull LS, Towns DR 2007c. Attempting to manage complex predator-prey interactions fails to avert imminent extinction of a threatened New Zealand skink population. Journal of Wildlife Management 71: 1576–1584.

Houck LD 2009. Pheromone communication in amphibians and reptiles. Annual Review of Physiology 71: 161–176.

Kats LB, Dill LM 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5: 361–394.

King CM (Editor) 2005. The handbook of New Zealand mammals. Oxford, Oxford University Press. 610 p.

Lima SL, Dill LM 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619–640.

Magurran AE 1999. The causes and consequences of geographic variation in antipredator behavior: perspectives from fish

populations. In: Foster SA, Endler JA eds. Geographic variation in behaviour: perspectives on evolutionary mechanisms. New York, Oxford University Press. Pp. 139–163.

Mason RT, Parker MR 2010. Social behavior and pheromonal communication in reptiles. Journal of Comparative Physiology A 196: 729–749.

Meyer-Rochow VB 1988. Behaviour of young tuatara (*Sphenodon punctatus*) in total darkness. Tuatara 30: 36–38.

Meyer-Rochow VB, Teh KL 1991. Visual predation by tuatara (*Sphenodon punctatus*) on the beach beetle (*Chaerodes trachyscelides*) as a selective force in the production of distinct colour morphs. Tuatara 31: 1–8.

Murray DL, Roth JD, Wirsing AJ 2004. Predation risk avoidance by terrestrial amphibians: the role of prey experience and vulnerability to native and exotic predators. Ethology 110: 635–647.

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

Nolte DL, Mason JR, Epple G, Aranov E, Campbell DL 1994. Why are predator urines aversive to prey? Journal of Chemical Ecology 20: 1505–1516.

Schwenk K 1995. Of tongues and noses: chemoreception in lizards and snakes. Trends in Ecology & Evolution 10: 7–12.

Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119: 610–621.

Stone PA, Snell HL, Snell HM 1994. Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. Conservation Biology 8: 569–573.

Strauss SY, Lau JA, Carroll SP 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecology Letters 9: 354–371.

Tingley R, Thompson MB, Hartley S, Chapple DG 2016. Patterns of niche filling and expansion across the invaded ranges of an Australian lizard. Ecography 39: 270–280.

Towns DR 1996. Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific rat *Rattus exulans*. Pacific Conservation Biology 2: 286–292.

Towns DR, Daugherty CH 1994. Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonisation. New Zealand Journal of Zoology 21: 325–339.

Van Damme R, Quick K 2001. Use of predator chemical cues by three species of lacertid lizards (*Lacerta bedriagae*, *Podarcis tiliguerta*, and *Podarcis sicula*). Journal of Herpetology 35: 27–36.

Walls GY 1981. Feeding ecology of the tuatara (*Sphenodon punctatus*) on Stephens Island, Cook Strait. New Zealand Journal of Ecology 4: 89–97.

Whitaker AH 1972. Lizard predators. Pepeke 19: 4–5.

Wirsing AJ, Roth JD, Murray DL 2005. Can prey use dietary cues to distinguish predators? A test involving three terrestrial amphibians. Herpetologica 61: 104–110.

Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH 2008. Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. Proceedings of the National Academy of Sciences 105: 7676–7680.

Worthy TH, Holdaway RN 2002. The lost world of the moa. Prehistoric life of New Zealand. Bloomington, Indiana, Indiana University Press. 718 p.