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RESEARCH

Twenty years on: changes in lizard encounter rates following eradication of rats from Kāpiti Island

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Abstract: Introductions of mammalian predators have led to extinctions or declines of many species on islands; hence eradications of these mammals have played a major role in biodiversity conservation. However, eradications are costly and sometimes controversial. It is therefore important to conduct carefully designed sampling programmes that allow benefits to native species to be quantified. We report the results of sampling conducted in 1994–1996 and 2014–2015 to estimate changes in relative abundance of lizards on Kāpiti Island over 20 years following the eradication of Norway rats (*Rattus norvegicus*) and kiore (*Rattus exulans*) in 1996. Sampling was conducted in five different habitats over the island, and in each habitat involved repeatedly sampling 4–5 pitfall stations (five pitfall traps each) and conducting spotlighting and daytime searches along 2–3 transect lines. We used generalised linear mixed modelling to estimate proportional changes in lizard encounter rates while accounting for effects of month, weather variables, and changes in vegetation density. Pitfall capture rates for northern grass skinks (*Oligosoma polychroma*), brown skinks (*Oligosoma zelandicum*), and copper skinks (*Oligosoma aeneum*) were estimated to increase 2- to 28-fold in habitats where they were detected in 1994–1996, and these species were also found in 2014–2015 in habitats where they were not detected in 1994–1996. Spotlighting encounter rates for geckos (predominantly Raukawa geckos, *Woodworthia maculata*) were estimated to increase 3.7-fold between the two time periods. There were sparse observations of ornate skinks (*Oligosoma ornatum*), forest geckos (*Mokopirirakau granulatus*) and Wellington green geckos (*Naultinus punctatus*), whereas goldstripe geckos (*Woodworthia chrysosiretica*), which were discovered on the island in 2013, were not detected in the areas sampled. Most lizards continue to be found in habitats with low, dense vegetation, a pattern that may be at least partially attributable to predation pressure from the abundant weka (*Gallirallus australis*) on the island.

Keywords: Kāpiti Island, lizard abundance, long-term studies, pitfall trapping, rodent eradication, spotlighting

Introduction

Introduced predators are known to severely impact ecosystems, and their removal often results in increased abundance of vulnerable species, particularly on islands (Jones et al. 2016). Before humans colonised New Zealand, lizards were widespread throughout a range of ecosystems on the mainland (North, South and Stewart Islands) and on offshore islands, and would have played important functional roles as prey, predators, pollinators and seed dispersers (Hare 2016). However, the introduction of exotic mammals in combination with widespread land modification has greatly reduced the distribution and abundance of lizards, causing extinctions, isolated populations and range restrictions of many species (Hitchmough et al. 2016; Towns et al. 2016). Similar effects of introduced mammalian predators have been documented on island lizard faunas around the world, including islands in

the Sea of Cortez, Caribbean, Seychelles, Mascarenes, and the Galapagos (Case & Bolger 1991).

The impact of rodent introductions on lizards on New Zealand islands has been understood for at least 50 years. Through comparison of islands, Whitaker (1973, 1978) documented that both abundance and diversity of lizards was reduced when kiore (*Rattus exulans*) were present, with these islands typically having two to three fewer species than expected. He also documented that the effect of kiore differed among lizard species, with some severely impacted while others seemed to be unaffected (Whitaker 1978). Such impacts may be due to both predation and competition, as kiore would have reduced fruit and invertebrates that lizards would have fed on as well as directly preying on lizards.

The clearest evidence of rodent impacts comes from studies that compare lizard abundance before and after rat invasion or eradication, as these comparisons avoid the

confounding effects of other factors affecting the lizard faunas of different islands. After kiore invaded Lizard Island in 1977, pitfall capture rates declined from 2.3 lizards per10 trap days in 1973 to 0.2 lizards per10 trap days by 1984, and only three lizard species were recorded compared to the five recorded in 1973 (McCallum 1986). After the eradication of kiore from Korapuki Island in 1986, there were immediate increases in capture rates of coastal lizards such as shore skinks (*Oligosoma smithii*), and slower increases in capture rates in forested habitats (Towns 1991). Similarly, capture rates for McGregor's skinks (*Oligosoma macgregori*) and Raukawa (common) geckos (*Woodworthia maculata*) on Mana Island increased significantly after the eradication of house mice in 1989–1990 (Newman 1994). Similar patterns can occur in parts of mainland New Zealand with ongoing predator control. Lettink et al. (2010a) experimentally demonstrated that survival of McCann's skink (*Oligosoma maccanni*) could be increased through predator control in coastal duneland on the Kaitorete Spit, and Reardon et al. (2012) showed that population growth rates of grand skinks (*Oligosoma grande*) and Otago skinks (*O. otagense*) at Macraes Flat could be greatly increased through predator control. However, other studies have not found measurable benefits to lizards from predator control, both in predator exclosures and unfenced areas (Nelson et al. 2016).

Given that eradications are costly and sometimes controversial (Wallach et al. 2018), it is important to quantify their effects on native species, and where possible to do this using carefully designed sampling programmes that eliminate potential confounds. Here we report results of sampling conducted in 1994–1996 and 2014–2015 to estimate changes in lizard encounter rates on Kāpiti Island over 20 years following the eradication of Norway rats (*Rattus norvegicus*) and kiore in 1996.

Methods

Study site

Kāpiti is a 1965-ha island 5 km off the west coast of the lower North Island (40.85° S, 174.91° E) which was originally dominated by mature coastal and podocarp-mixed broadleaf forest. It has been occupied by Māori for many centuries, resulting in some vegetation impacts and introduction of kiore (Maclean 1999). Following European arrival, most of the forest was cleared for farming and the island was colonised by Norway rats, cats (*Felis catus*), brush-tailed possums (*Trichosurus vulpecula*), feral cattle (*Bos taurus*), goats (*Capra hircus*) and sheep (*Ovis aries*). Most of Kāpiti was designated a sanctuary in 1897 and mammal eradications began in 1902 (Fuller 2004). The final eradications occurred in 1996 when the two rat species were removed through an aerial poison operation (Miskelly & Empson 2004). There is ongoing monitoring for incursions, resulting in stoats (*Mustela erminea*) being eradicated after three animals were detected in 2010 (Prada et al. 2014). Kāpiti consists mostly of hilly terrain, which by 1996 was dominated by regenerating forest and shrubland, with abundant kohekohe (*Dysoxylum spectabile*), kānuka (*Kunzea ericoides*), tawa (*Beilschmiedia tawa*) and whauwhaupaku (five-finger, *Pseudopanax arboreus*). There are also three flat areas of grassland, and areas dominated by tussock and flax (harakeke *Phormium tenax* and wharariki *P. cookianum*) totalling about 60 ha.

Sampling design

Gorman (1996) developed a sampling design to enable quantitative comparison of lizard encounter rates before and after the 1996 rat eradication (Fig. 1, Appendix S1 in Supplementary Materials). This involved measuring encounter rates through pitfall trapping, spotlighting and daytime searching in six different habitats: (1) coastal grassland, which is a mixture of open grassland, tussocks, harakeke, shrubs and small trees near the coast at the north end of the island; 2) kānuka forest, which is an area of mature kānuka and mānuka (*Leptospermum scoparium*) at the north end of the island; (3) ridge grassland, which is located on a ridge near the summit (521 m asl) and is similar to the coastal grassland habitat but with wharariki also present; (4) coastal forest, which is a damp stony area near Rangatira Point dominated by karaka (*Corynocarpus laevigatus*), kawakawa (*Macropiper excelsum*), kohekohe, tarata (*Pittosporum eugenioides*) and māhoe (*Melictus ramiflorus*); (5) high forest, which is higher-altitude forest above Rangatira Point with abundant tawa (*Beilschmiedia tawa*), hīnau (*Elaeocarpus dentatus*), kānuka, kohekohe, māhoe, northern rātā (*Metrosideros robusta*) and rewarewa (*Knightia excelsa*), with any one species or assemblage generally only dominant in small patches; and (6) kohekohe forest, which was similar to high forest but with extensive areas of kohekohe dominated canopy. These six habitats were chosen to provide a logistically feasible
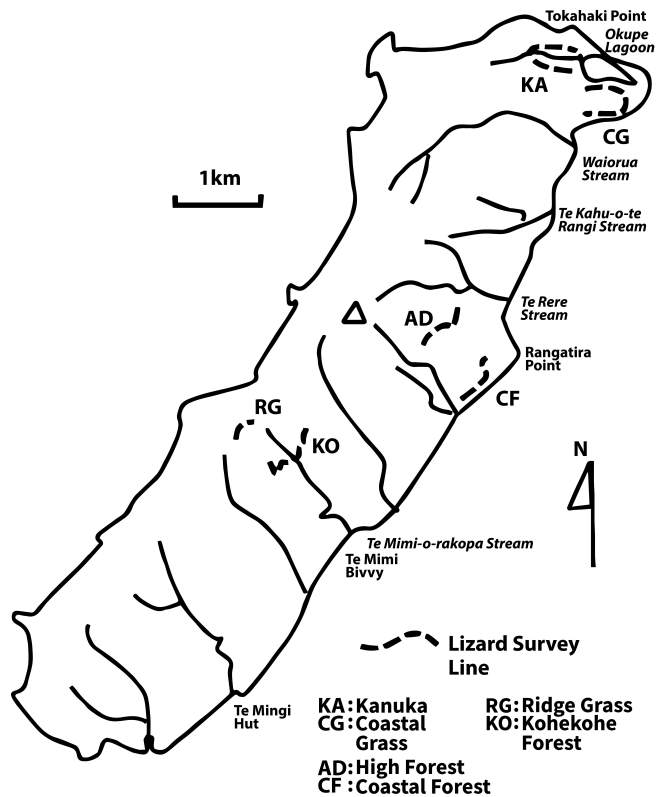
Figure 1. Lizard survey lines established in high forest (AD), coastal forest (CF), coastal grassland (CG), kānuka forest (KF), ridge grassland (RG) and kohekohe (KO) habitats in 1994. There were two 200-m transects and 4–5 pitfall stations along each of the lines shown (Appendix S1), with 5 pitfall traps at each station. Pitfall trapping, spotlighting and hand searching was conducted in all 6 habitats in 1994–1996, and repeated in five habitats in 2014–2015 (when KO was excluded due to safety concerns).

design that would be representative of the island's main habitat types, with survey locations aligned with rat traplines established for monitoring purposes in October 1992. Five of these habitats were re-sampled in 2014–2015 (Gollin 2016), with the kohekohe forest excluded due to safety concerns.

In each habitat there was usually 4-5 pitfall stations with five pitfall traps (Appendix S1, Appendix S2) and two 200-m transects for spotlighting and daytime searching. Nine pitfall stations were sampled in ridge grassland in 1994–1996 (Appendix S1). However, only five of these stations were re-sampled in 2014–2015 due to safety concerns with accessing the other stations, and this also meant that one of the two transect lines was not sampled. Otherwise, the locations sampled in 2014–2015 were the same as those sampled in 1994–1996, as identified by marker pegs and visual confirmation by NG (see Appendix S2). In addition to lizard sampling, we quantified vegetation cover in both 1994–1996 and 2014–2015 to assess whether changes in lizard counts were attributable to vegetation changes, and quantified weather to account for its potential confounding effects on counts. Data were collected by NG in 1994–1996 and JFG 2014–2015, but NG introduced JFG to all procedures to ensure consistency. Data collection took place from December 1994 to March 1995 and November 1995 to March 1996, and from November 2014 to April 2015. All data used in this study are available in Appendix S2.

Data collection

Pitfall traps
We collected pitfall data from each station over 28 sampling sessions in 1994–1996 and 6 sampling sessions in 2014–2015. The five pitfall traps in each station consisted of a central pitfall trap with the rest placed in a cross formation 4 m from the central pitfall trap. The traps were removed in March 1996 to avoid lizard mortality and replaced with new ones in October 2014. However, the positions were similar, as the position of the central trap was marked with a peg. In both cases the traps consisted of 4-L paint tins with drainage holes cut in the bottom and were dug into the ground or into rock piles until the rim was flush with the ground surface. Small pieces of stone, wood or leaves were placed in the bottom to provide cover for lizards, and rocks or pinned-down plywood were used to cover the traps. When the traps were not set, they were left with large sticks or rocks in them to allow animals to escape. When the traps were set, the escape paths were removed and a teaspoon each of canned pear and a chicken-or fish-based cat food placed at the bottom of the pitfall trap. The traps were checked within 24 h after setting. Each lizard caught was identified to species, then released approximately 0.5 m from the trap where it was caught.

Spotlighting
We collected spotlighting data from each transect on two occasions in 1994–1996 and 2–3 occasions in 2014–2015. This involved slowly walking the 200-m transect over about 2 h, starting shortly after it was completely dark. We used a head lamp and binoculars, aiming the light toward the ground, tree trunks, crevices and canopy as well as looking in shrubs and flax bushes where present. We only conducted spotlighting when vegetation was dry, as water droplets make eyeshine difficult to distinguish.

Daytime searching
We searched the same transects by day on 1–2 occasions in 1994–1996 and two occasions in 2014–2015, except for the

ridge grassland transect which was not searched. This involved searching for 1–2 h at times when lizards were expected to be active (no rain or wind), but the methods differed among habitats due to differences in vegetation structure. In coastal forest, kānuka forest and high forest, we searched within 5 m of the track, looking in or under potential lizard retreats, including rocks, logs, fallen bark, leaf litter, and tree crevices, and scanned foliage and canopy with binoculars. In coastal grassland, where the vegetation consisted of long grass and shrubs, the ground and vegetation were scanned by 2–3 observers walking 5 m apart with similar total search effort in each instance.

Vegetation cover
We quantified vegetation cover in a circle of 6-m radius centred at the central pitfall trap for five strata: ground layer (plants < 0.3 m high), large herbs and tussocks < 3 m, shrubs (0.3 to 2 m high), small trees (> 2 m high but < 10 cm diameter at breast height) and trees (> 10 cm diameter at breast height). We scored each stratum on the Braun-Blanquet scale (Moore 1962) where 0 = scarce or isolated, 1 < 5% cover, 2 = 5–25% cover, 3 = 25–50% cover, 4 = 50–75% cover, and 5 = 75–100% cover.

Weather variables
For each day that sampling took place, we obtained data on the maximum and minimum temperature, and relative humidity in the morning (06:00), midday and evening (18:00) from the nearest CliFlo NIWA weather stations (station 3145 Paraparaumu Aero and station 17029 Wallaceville Ews). We also scored the general weather conditions each day as: 0 = constant rain or mist, 1 = overcast with some rain, 2 = mostly cloudy, 3 = mostly fine, 4 = fine all day.

Data analysis
We analysed data using OpenBUGS version 3.2.3 (Spiegelhalter et al. 2014), which is a Bayesian updating software package that is particularly effective for hierarchical modelling. We only fitted models to pitfall data for skinks and spotlighting data for geckos, as other data were too sparse. The response variables were counts, i.e. the number of skinks caught in a pitfall in 24 h or the number of geckos seen on a transect in one night. We therefore analysed these data using generalised linear mixed models with Poisson error terms and log link functions. Consequently, we could easily derive the proportional changes in encounter rates from 1994–1996 to 2014–2015 while accounting for effects of weather and month. These proportional changes will reflect changes in relative abundance of lizards if encounter rates are proportional to density when confounding effects are accounted for (Williams et al. 2002, p. 258).

For pitfall counts, we did separate analysis for each skink species for each of the three habitats they were found in. We always included the time period (1994–1996 or 2014–2015) and month as categorical fixed effects, and the pitfall station and individual pitfall trap as hierarchical random effects. We added weather variables as standardised covariates if they were found to significantly affect counts (i.e. 95% credible intervals did not overlap 0). We initially fitted models without vegetation scores, then added those scores to the models (as standardised covariates) to assess whether changes in skink counts were attributable to vegetation changes.

Because spotlighting counts were sparser, we did a single analysis for these data with time period, month, and weather variables as fixed effects, and transect as a random effect. Vegetation variables were not included in spotlighting analysis as these data were only collected for the pitfall stations.

Models were updated for 10 000 Markov Chain Monte Carlo (MCMC) iterations following a burn-in of 5000 iterations, using two chains to check for convergence.

Results

Most skinks encountered were captured in baited pitfall traps (Table 1, Fig. 2). Almost all these captures were Northern grass skinks (*Oligosoma polychroma*) ($n = 506$), brown skinks (*O. zelandicum*) ($n = 19$), or copper skinks (*O. aeneum*) ($n = 67$), caught in the coastal grassland ($n = 419$), ridge grassland ($n = 158$) and kānuka forest ($n = 15$) habitats. A single ornate skink (*O. ornatum*) was caught in a baited pitfall trap in coastal forest in 2014–2015, whereas none were caught in 1994–1996. We recorded only 17 skinks in daytime searches, including 6 found in 30.8 h of searching in 1994–1996 and 11 found in 30.3 h of searching in 2014–2015. Most of these fled before they could be identified.

Most geckos were encountered during spotlighting ($n = 129$) and daytime searching ($n = 25$), including 69 in coastal grassland, 27 in kānuka forest, 24 in ridge grassland, 6 in coastal forest, and one in high forest. The gecko in high forest was a forest gecko (*Mokopirirakau* "Southern North Island") which was found in 1994–1996. The remainder appeared to be Raukawa geckos (*Woodworthia maculata*), and this was confirmed for the 37 individuals that were captured. Four Raukawa geckos were captured in pitfall traps. There were also two incidental sightings of Wellington green geckos (*Naultinus punctatus*) in 2014–2015, one in the kānuka forest habitat and the other by the lodge at the north end of the island.

Skink pitfall-trap capture rates

In coastal grassland, grass skinks and brown skinks were estimated to increase about 2-fold from 1994–1996 to 2014–2015, although the increase for the latter species is insignificant, i.e. the 95% credible interval for the proportional change includes 1 (Table 1, Fig. 2). Copper skinks, which only had 3 captures in 1994–1996, were estimated to increase almost 30-fold.

In ridge grassland, grass skinks were estimated to increase 6-fold from 1994–1996 to 2014–2015. Brown and copper
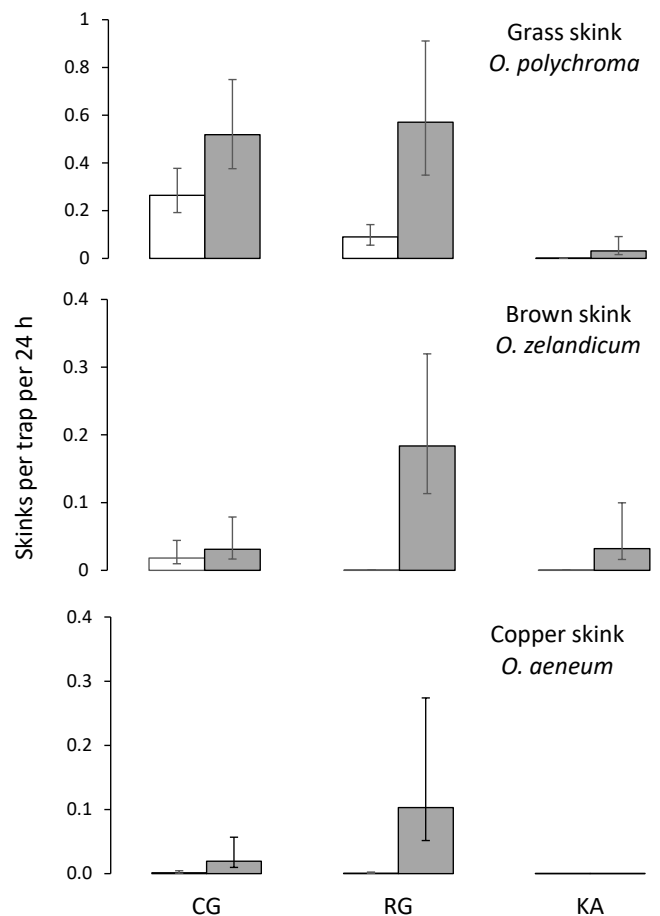
Figure 2. Changes in capture rates of three *Oligosoma* species in pitfall traps on Kāpiti Island between 1994–1996 (white) and 2014–2015 (grey). Most skinks were caught in the three habitats shown: coastal grassland (CG), ridge grassland (RG) and kānuka forest (KA); one ornate skink (*O. ornatum*) was captured in coastal forest in 2014–2015 and no skinks were caught in high forest. Estimates shown are for an average pitfall trap in average weather in February based on hierarchical Poisson regression models, with error bars indicating standard errors (asymmetric due to log link function).

Table 1. Changes in relative abundance of three *Oligosoma* species in three different habitats on Kāpiti Island between 1994–1996 and 2014–2015, assuming densities are proportional to capture rates in pitfall traps when effects of month and weather are accounted for. Poisson regression models were run with and without vegetation variables to assess whether changes in skink abundance were attributable to changes in vegetation. The estimated changes are proportional, so can be considered statistically significant if the 95% credible interval (CRI) does not include 1.
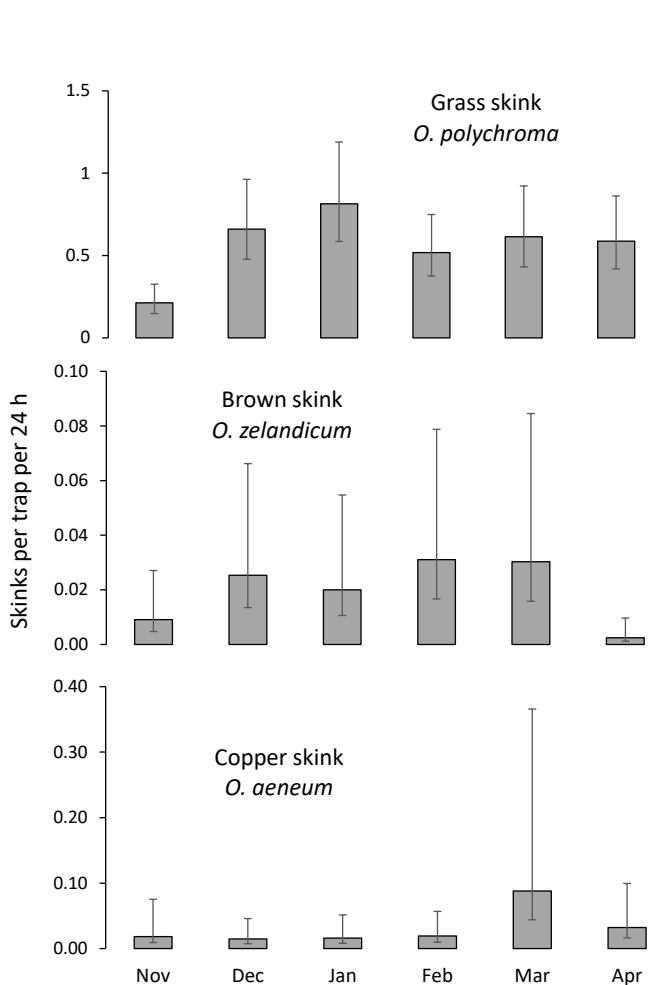
Habitat	Species	No vegetation variables		With vegetation variables	
		Estimate	95% CRI	Estimate	95% CRI
Coastal grassland	*O. polychroma*	2.0	1.5–2.5	13.3	5.4–28.6
	O. zelandicum	1.8	0.8–3.7	7.0	0.4–32.8
	O. aeneum	28.3	3.6–119	15.4	0.1–83.7
Ridge grassland	*O. polychroma*	6.4	4.1–9.5	8.4	4.7–13.9
	*O. zelandicum**	$5×10^7$	$109–5×10^7$	$2×10^8$	$137–9×10^7$
	*O. aeneum**	$9×10^6$	$13.1–2×10^7$	$3×10^8$	$19.0–1×10^7$
Kānuka forest	*O. polychroma**	$3×10^6$	$22.4–4×10^6$	$3×10^4$	$0.2–1×10^5$
	*O. zelandicum**	$1×10^7$	$27.1–2×10^7$	$6×10^5$	$0.9–2×10^6$

* shows cases where no skinks were caught in 1994–1996

skinks were not detected in this habitat until 2014–2015, hence the proportional increases are difficult to interpret. However, these increases were clearly significant (Table 1).

In kānuka forest, no skinks were detected in 1994–1996, whereas small numbers of grass skinks (8) and brown skinks (7) were caught in 2014–2015. The proportional increases in this habitat are, therefore, difficult to interpret but are clearly significant (Table 1).
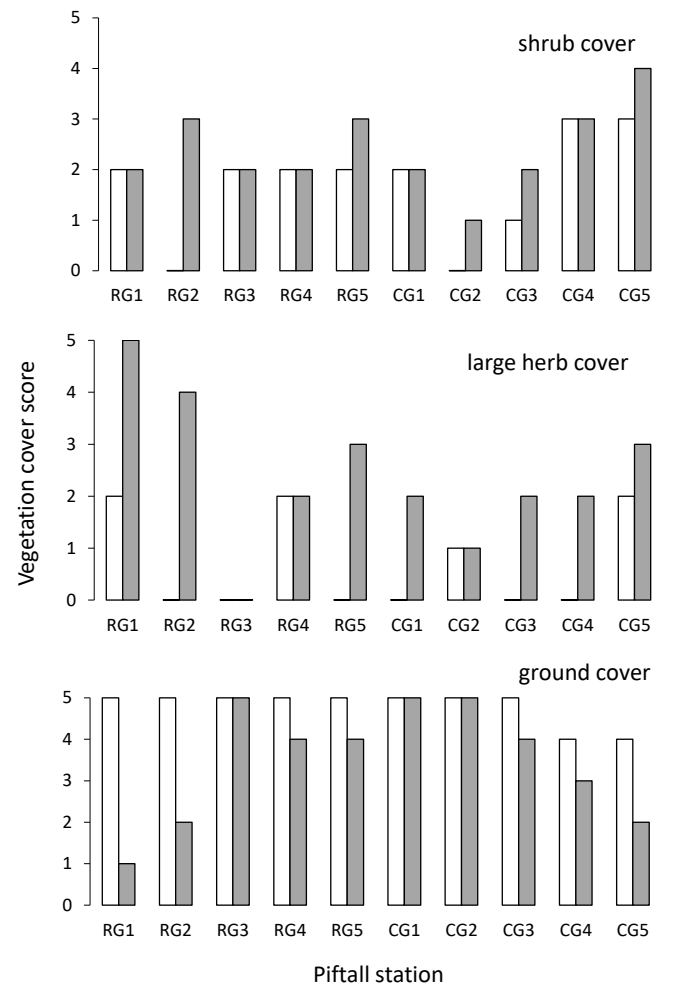
Skink capture rates were significantly affected by month and weather; hence it was important to account for these variables. Random variation among pitfall stations and individual traps was also evident based on the posterior distributions for these random effects. Seasonal patterns varied somewhat among species. For example, in coastal grassland, where sample sizes were highest, capture rates were consistent from December–April for grass skinks, whereas they dropped off at the end of this period for brown skinks and increased for copper skinks (Fig. 3). Capture rates were consistently positively correlated with weather scores. For example, in coastal grassland capture rates for grass skinks and brown skinks were estimated to increase 1.3-fold (95% CRI 1.2–1.5) and 1.9-fold (1.2–3.3) respectively with each 1 SD increase in weather score. The effects of the other weather variables were generally insignificant so were excluded from the models.

The key vegetation change from 1994–1996 to 2014–2015 was a marked increase in large herb cover at almost all pitfall stations (Fig. 4, Fig. 5). There was a corresponding reduction in ground cover at the coastal grassland and ridge grassland stations, but not in kānuka forest. Changes in other layers were minor, but there was a tendency for shrub cover to increase in all habitats and tree cover to reduce in kānuka forest.

Vegetation scores were not generally significant predictors of skink capture rates, so had little effect on interpretation of changes in relative abundance of skinks. However, capture rates of grass skinks and brown skinks in coastal grassland both increased significantly with increasing ground cover, and capture rates of grass skinks also decreased significantly with increasing large herb cover. Because ground cover declined and large herb cover increased in this habitat from 1994–1996 to 2014–2015, the estimated vegetation-specific increases in relative abundance of grass and brown skinks are much higher than the estimated increases when vegetation change is not accounted for (Table 1). Incorporating vegetation scores also reduced power where sample sizes are low; i.e. the increases in relative abundance of skinks in kānuka forest become insignificant when vegetation changes are included in the model, and this is also the case for copper skinks in coastal grassland.


Figure 3. Seasonal patterns in capture rates of three *Oligosoma* species in pitfall traps on Kāpiti Island. Estimates (with standard errors) are for coastal grassland in 2014–2015, using the same hierarchical Poisson regression models as in Figure 2.

Figure 4. Comparisons of Braun-Blanquet scores for vegetation cover in ridge grassland (RG) and coastal grassland (CG) between 1994–1996 (white) and 2014–2015 (grey) for three vegetation layers. A pitfall station is a collection of five pitfall traps.
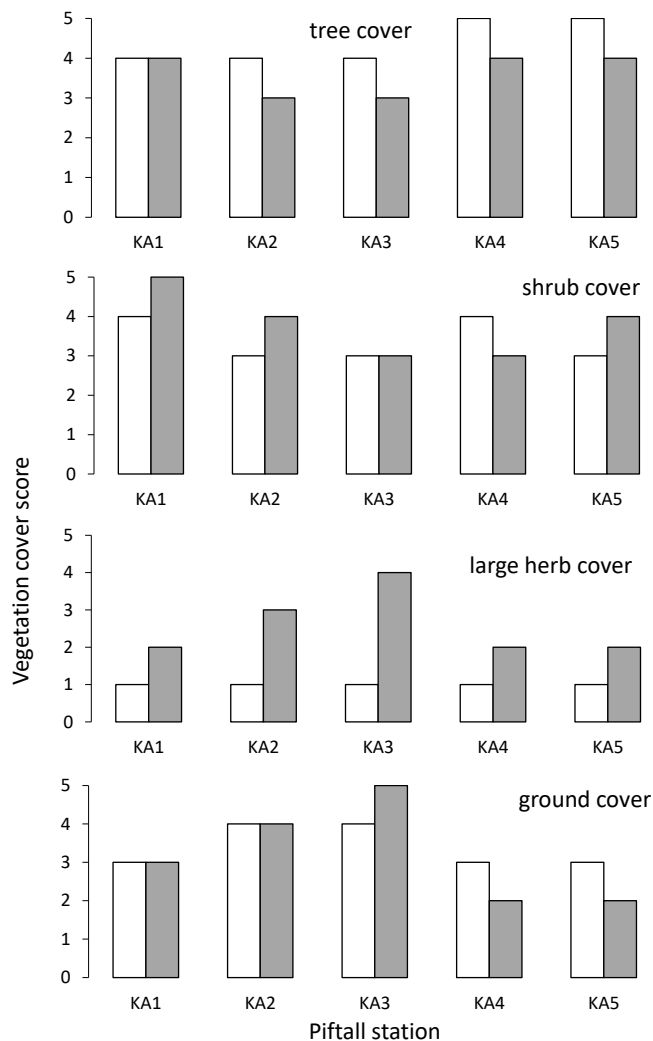
Figure 5. Comparisons of Braun-Blanquet scores for vegetation cover in kānuka forest between 1994-1996 (white) and 2014-2015 (grey) for four vegetation layers. A pitfall station is a collection of five pitfall traps.

Gecko spotlighting encounter rates

The gecko encounter rate in spotlighting surveys increased 3.7-fold (95% CRI 1.8–7.6) from 1994–1996 to 2014–2015, with sightings occurring in one new habitat (coastal forest) in 2014–2015. There was clear variation among transects, as is reflected in the numbers found in the five habitats as reported above. Spotlighting encounter rates did not vary significantly among months or with weather variables.

Discussion

The data from pitfall traps and spotlighting on Kāpiti Island show that lizard abundance has increased since the 1996 rat eradication, at least in some habitats. The data show 2- to 28-fold increases in habitats where species were detected in 1994–1996 if encounter rates are proportional to density when weather and season are accounted for. However, it is important to acknowledge that changes in encounter rates could also potentially reflect changes in detection, and this potential confound can only be eliminated using mark-capture

or other methods allowing detection probability to be quantified (Williams et al. 2002). There is no obvious reason to expect detection rates through pitfall captures to change, for example due to changes in vegetation structure and composition. However, it is quite possible that the probabilities of gecko being detected during spotlighting has increased due to behavioural changes in the absence of rats (Hoare et al. 2007).

Species were also encountered in new habitats in 2014–2015, i.e. brown and copper skinks in ridge grassland, brown and grass skinks in kānuka forest, and Raukawa geckos in coastal forest. It is impossible to know whether these species were completely absent from these habitats before the rat eradication, but the increases are statistically significant at least for the skink species. Ornate skinks still appear to be at low density, with no evidence of increase (there were a few incidental observations of ornate skinks in both 1994–1996 and 2014–2015, as well as the single pitfall capture 2014–2015). Ornate skinks were not expected to occur in the dry coastal grassland and ridge grassland habitats. They were also not expected to be common in the forest habitats given that forest typically has low densities of lizards regardless of impacts of introduced predators (Whitaker 1978). It is also impossible to make inferences from the few sightings of forest geckos and green geckos, which are difficult to detect without intensive monitoring focused on these species. The only other lizard species known to occur on Kāpiti, the goldstripe gecko (*Woodworthia chrysosiretica*), was not detected in either 1994–1996 or 2014–2015. Goldstripe geckos were discovered in 2013 in flax habitat at the south end of the island and on the summit ridge at the head of the Taepiro. However, they have not been detected in the habitats sampled in our study (Barr et al. 2013).

Prior to their eradication, Norway rats and kiore were both found year-round in all habitats sampled in our study, with the highest, but most variable capture rates in coastal grassland and kānuka forest while more stable, lower-density populations were found in forested habitats (Dick 1985). Norway rats were estimated to have higher density than kiore, and both species were competitors and predators of lizards on Kapiti. Both species' diets are a mix of plant material, invertebrates, and vertebrates. Stomach samples from Kāpiti suggested that invertebrates dominated the kiore diet and seed dominated the Norway rat diet, but skink remains were found in both species (Dick 1985).

Rodents may also affect lizards indirectly due to their impacts on plant communities through their consumption of vegetation, flowers, fruits, seeds, pollinators and seed dispersers (Campbell 1978; Campbell & Atkinson 2002; Graham & Veitch 2002; McClelland 2002). Lizards select microhabitats where they can optimise foraging, thermoregulation and predator avoidance, so changes in vegetation structure can affect lizard species differently (Stephens 2004). Our vegetation data suggest changes in vegetation structure since the rat eradication, although it is unknown whether those changes are due to rat removal or to longer-term succession changes due to past land clearance or other impacts. These vegetation changes do not explain the observed increase in lizards. Rather, the observed increases in large herb cover and decreases in ground cover were estimated to have made habitats less suitable for skinks based on the relationships between capture rates and vegetation characteristics at pitfall stations. For brown and grass skinks in coastal grassland, the vegetation-specific skink increases (i.e. with vegetation variables included in models) are estimated to be much greater than the overall increases

(i.e. excluding vegetation variables), suggesting these species have increased in abundance despite the changes in vegetation, not because of them.

Given the responses of lizard populations to rodent eradications observed elsewhere, the observed increase in lizard abundance since 1996 is unsurprising. However, recovery on Kāpiti Island appears to have been less than at other sites and confined to particular species and habitat types. On Korapuki Island, lizard pitfall captures at a coastal site increased consistently following eradication of kiore, with an almost 10-fold increase over three years (Towns 1991) and a 30-fold increase after 6 years (Towns 1994). In forested sites on the same island there was no measurable increase in lizard captures until six years after the eradication when a sudden increase (up to 10-fold) was observed (Towns 1994). Capture rates for ornate skinks in Zealandia Sanctuary approximately 20 years after eradication of rats and most other invasive mammals were 0.13 captures per pitfall per 24 h in a mouse exclosure and 0.064 captures per pitfall per 24 h outside the exclosure (Nelson et al. 2016). In comparison, on Kāpiti Island this species remains close to undetectable with the one pitfall capture in Coastal Forest in 2014–2015 equating to 0.0015 captures per pitfall per 24 h in that habitat, and 0.0005 captures per pitfall per 24 h over the three forest habitats. Kāpiti does not have mice but has an abundance of predatory birds.

Birds are natural and important predators of New Zealand lizards. Of those species listed by van Winkel & Ji (2012) as known predators of New Zealand lizards, 10 occur either naturally or as introduced populations on Kāpiti Island: blackbirds (*Turdus merula*), starlings (*Sturnus vulgaris*), koekoeā (long-tailed cuckoo, *Eudynamys taitensis*), ruru (morepork, *Ninox novaeseelandiae*), kārearea (New Zealand falcon, *Falco novaeseelandiae*), kahu (swamp harrier, *Circus approximans*), kōtare (New Zealand kingfisher, *Todiramphus sanctus*), pukeko (*Porphyrio melanotus*), takahē (*Porphyrio hochstetteri*) and weka (*Gallirallus australis*). Most of these species are also present at Zealandia apart from weka which have failed to establish following translocation attempts and koekoeā (Lynch 2019), while on Korapuki, blackbirds, starlings, koekoeā, ruru, kahu and kōtare have all been recorded (Hicks et al. 1975, Towns & Atkinson 2004). In sites where introduced predators have been eradicated, New Zealand bird populations can reach very high densities. Although these predator-prey relationships have evolved naturally, this predation may still reduce the restoration of vulnerable lizard populations and decrease the quality of habitat available to them. On Tiritiri Mātangi, lizard remains were not found in harrier or morepork pellets or pukeko faeces but were present in 88% of kingfisher pellets and in 60% of nests, suggesting they could have significant impacts on lizards (van Winkel & Ji 2012). If avian predation accounts for the differences in lizard recovery seen on Kāpiti Island compared to elsewhere, the most significant factor is likely to be the presence of weka.

Weka are known to be predators of ground-nesting birds, lizards, insects and snails, leading to their eradication from many New Zealand islands (Miskelly & Beauchamp 2004). Introduced weka appear to have had a major impact on lizards on the Open Bay Island (Lettink et al. 2010b). Weka are also believed to have been introduced to Kāpiti before it became a reserve. They are seen actively foraging on Kāpiti day and night, frequently turning over cover such as leaf litter and beach wrack. We observed weka foraging in all the habitats sampled in this study, but especially in the forested habitats, potentially explaining the scarcity of ornate skinks in coastal

forest and high forest, and the scarcity of other skinks in kānuka forest. In addition, skinks are likely to be much more vulnerable to weka predation in forest than in the grassland habitats where the dense ground vegetation offers protection. Whitaker (1995) predicted that lizard recovery on Kāpiti would be compromised by the presence of weka. Data from a 5-year weka-exclosure experiment on Kāpiti immediately after the rat eradication suggested that lizard densities were unaffected by weka (Miskelly & Beauchamp 2004). This could potentially mean that the scarcity of lizards in forest is due to other factors but could also reflect the experiment's short time scale in relation to expected lizard recovery rates.

The species most vulnerable to weka may be those that were most vulnerable to rats, i.e. large terrestrial species (Whitaker 1978). The eight lizard species currently known on Kāpiti represents a low diversity compared to the number expected based on the island's size and habitat diversity (Gorman 1996), and these surviving species are all relatively tolerant of rat predation. It is therefore likely that several species were eradicated by rats, other predators, and habitat destruction, or reduced to densities so low that their presence has not yet been confirmed. The latter may be the case for Duvaucel's gecko (*Hoplodactylus duvaucelii*), as Whitaker (1995) detected eye reflection from a large gecko at the top of the western cliffs above Taepiro stream. The other species likely to have been eradicated from Kāpiti, or still present at low densities, are the Pacific gecko (*Dactylocnemis pacificus*), southern striped gecko (*Toropuku stephensi*), northern spotted skink (*Oligosoma kokowai*), Kupe skink (O. aff. *infrapunctatum* "Southern North Island"), Whitaker's skink (*O. whitakeri*), and McGregor's skink (*O. macgregori*).

These species are all potential candidates for reintroduction to Kāpiti (or reinforcement translocation if still present) as there appears to be structurally suitable habitat for them (Brown et al. 2016). However, such translocations would only be considered if animals were released into weka-proof exclosures. While all of these species will have co-existed with weka and other avian predators in the past, to establish new populations in the presence of weka may require secure habitat large enough to support a sustainable population as an ongoing source of dispersal. Kupe skink and northern spotted skink could potentially persist in the presence of weka given that they occur in low dense vegetation such as coastal grassland and ridge grassland, where our results show that other skink species have significantly recovered since the rat eradication. However, it would nevertheless be preferable to also initially reintroduce these species to weka-proof enclosures, especially the rare Kupe skink. Regardless of the management inventions undertaken, the long-term monitoring protocols presented here provide a good basis for continuing to quantify changes in Kāpiti lizard populations and emphasise the importance of long-term data for assessing recoveries of taxa with slow population growth rates.

Author contributions

JG conducted the 2014–2015 fieldwork and initial data analysis, and wrote the thesis that this paper was based on; NG designed the study, completed 1994–1996 fieldwork, and contributed to paper drafts; DA conducted the analyses presented here and wrote the paper.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Distribution of lizard pitfall traps at Rangatira Point (a), North End (b) and Te Mimi grassland (c) on Kapiti Island in relation to walking tracks and other geographical features.

Appendix S2. Zipped .csv files containing data on locations of pitfall stations and line transects, and raw data on weather, pitfall captures, spotlighting encounters, and daytime search encounters.

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