Does the invasive plague skink (*Lampropholis delicata*) compete with native skink species in New Zealand?

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Abstract Invasive species are a major threat to biodiversity worldwide, causing many of the recent declines and extinctions of native species. Competition is a common mechanism through which invasive species impact the native biota. In particular, exploitative competition results when the invader outcompetes native species for essential resources, such as food and shelter sites. Despite being pervasive invaders, the ecological impacts of invasive lizards are understudied and it is often unknown whether these invaders have detrimental impacts. The plague skink (*Lampropholis delicata*), native to eastern Australia, has invaded several locations throughout the Pacific region (Hawaiian Islands, New Zealand, Lord Howe Island). However, no studies have documented the plague skink as having a negative impact on native species anywhere throughout its introduced range. Here, we conducted a mark-recapture study in northern New Zealand (Shakespear Regional Park) to investigate whether the plague skink competes with native skink species (*Oligosoma aeneum*, *O. ornatum*, *O. moco*). Though the plague skink has a broader distribution within the study region and occurred across a broader range of habitats, there was substantial range and niche overlap between the plague skink and the three native skink species. Both the absolute capture rates and estimated population size of the plague skink were significantly higher than the three native skink species. Although plague skinks have smaller body sizes well as shorter and narrower heads than the native skink species, there was still considerable scope for dietary overlap among the species. While our study does not provide definitive evidence for competition between the plague skink and native skink species in New Zealand, we clearly demonstrate the presence of the core components required for exploitative competition to occur. Further field- and laboratory-based studies will be required to confirm the existence of exploitative or interference competition by the plague skink in its introduced range.

Key words: biological invasion, habitat overlap, lizard, mark-recapture, New Zealand.

INTRODUCTION

Invasive species, those that have been introduced to a new region and successfully established and spread in areas outside of their native distribution (Blackburn *et al.* 2011; Chapple *et al.* 2012), are a major driver of native species decline and extinction globally (Blackburn *et al.* 2004; Towns *et al.* 2006; McGeoch *et al.* 2010; Doherty *et al.* 2016). The two main mechanisms through which invasive species impact the native biota are predation and competition (Mack *et al.* 2000; Kraus 2015); however, the consequences of each are generally different (David *et al.* 2017). Predation is generally responsible for the most severe impacts (particularly species extinctions) on native species, but while competition can negatively affect native species, its impacts are usually more subtle

and rarely lead to extinctions (Kraus 2015; David *et al.* 2017). However, while it is relatively straightforward to document the impact of predation, either through experimental or diet studies (Towns *et al.* 2006; Murphy *et al.* 2019; Woinarski *et al.* 2020, 2018, 2020), it is substantially more difficult to conclusively demonstrate the existence of competition (Blackburn *et al.* 2009; Doherty *et al.* 2016). As a result, there is a dearth of studies fully documenting cases of interspecific competition between native and invasive species (David *et al.* 2017).

Within both natural and invasive contexts, interspecific competition can structure communities, with competitive exclusion influencing species range limits and geographic diversity patterns (Wisz *et al.* 2013). Interspecific competition is the most probable mechanism of impact in instances where invasive species have numerical dominance over resident species within the same trophic level or guild (e.g. Reitz & Trumble 2002). It occurs when two or more species utilise the same resource, such as food or shelter sites

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and results in reduced competitor fitness (Mack *et al.* 2000). Competition may be classed as either interference or exploitative. Exploitative competition occurs through the consumption of a common resource (David *et al.* 2017). For example, this was experimentally demonstrated in manipulations of invasive larval bullfrog (*Rana catesbeiana*) density, where high densities of larvae depleted the algal food source, reducing survival and growth rates of native larval frogs (Kupferberg 1997). Interference competition, on the other hand, occurs in the case of direct negative interactions between species, for example when fighting occurs (David *et al.* 2017). Interference competition for food has been demonstrated between invasive Argentine ants (*Linepithema humile*) and native ant species. Here, it was found that natives were displaced in 60% of the occasions (Human & Gordon 1996).

Invasions by squamate reptiles are poorly known and are largely understudied (Kraus 2009, 2015). Invasive lizards generally have a generalist diet, are highly fecund and often small or cryptic in nature, allowing invaders to utilise local resources and undergo rapid population growth largely unnoticed by biosecurity or management authorities (Kraus 2015). There are nine invasive lizard species globally that have known ecological impacts, with nearly all (eight) occurring through competition rather than predation (Kraus 2015). One of the best studied invasive lizards is the Asian house gecko (*Hemidactylus frenatus*), which has been responsible for population declines in native species in several locations worldwide (Petren & Case 1996; Cole *et al.* 2005). Experiments in Hawaii demonstrated that the presence of *H. frenatus* depressed the mean body condition and survival of the resident species *Lepidodactylus lugubris* (mourning gecko), due to asymmetric exploitative competition (Petren & Case 1996). Similarly, in Guam, the invasive curious skink (*Carlia ailanpalai*) has reached extremely high population densities, and due to their sheer numbers may out-compete native species for food or physically displace them following territorial interactions (Campbell 1996).

The plague skink (*Lampropholis delicata*), also known as the delicate skink or rainbow skink, is a species that has successfully invaded several locations throughout the Pacific region (Lever 2003; Kraus 2009; Chapple *et al.* 2013a). Native to eastern Australia, the plague skink has become invasive in the Hawaiian Islands (introduced ~1905; Baker 1979), New Zealand (mid-1960s; Chapple *et al.* 2013a; Chapple *et al.* 2016a) and Lord Howe Island (1980s; Moule *et al.* 2015; Chapple *et al.* 2016b) via human-mediated dispersal (Chapple *et al.* 2016b, 2016b). Although studies are yet to confirm or quantify any negative impact of plague skinks on the native biota

(Chapple *et al.* 2016a), several presumed or potential impacts have been suggested based on anecdotal information. However, the high density of plague skinks on Lord Howe Island has been used to infer that they may have a negative impact on the endemic invertebrate fauna (Chapple *et al.* 2016b). Similarly, initial speculation (Hunsaker & Breese 1967; Baker 1979) that the arrival of the plague skink in the Hawaiian Islands was the cause of the rapid population crashes of two resident skink species (*Lipinia noctua*, *Emoia impar*); however, this hypothesis has since been discounted (Fisher & Ineich 2012). The absence of strong evidence for the impact of the plague skink on the native biota may largely be due to the lack of dedicated studies (but see Peace 2004). There are no native lizard species in Hawaii (Baker 1979; Chapple *et al.* 2013a), and the only two native lizard species on Lord Howe Island have a different activity pattern to the plague skink (Chapple *et al.* 2016b). Thus, as New Zealand has a diverse native lizard fauna (100+ species; ~65 skinks, ~45 geckos; Chapple 2016; Hitchmough *et al.* 2016a), it presents the ideal location in which to investigate the impact of the plague skink on native lizard species.

The plague skink was first detected in New Zealand at the Otahuhu railyards in south Auckland in the mid-1960s (A.H. Whitaker, pers. comm. in Lever 2003). Over the subsequent ~50 years, it spread across the majority of the North Island, and more recently into a couple of locations in the South Island (Chapple *et al.* 2016a; D. van Winkel, unpubl. data). Modelling suggests that the plague skink has the potential to spread further throughout both the North and South Islands (Tingley *et al.* 2016). The spread of the species was potentially aided by it being listed in the *Wildlife Act 1953* until 2010, when they were moved to Schedule 5 ('wildlife not protected') of the Wildlife Act and simultaneously listed as an 'unwanted organism' under the *Biosecurity Act 1993*. This shift in legal status was motivated by recognition of the potential threat of the plague skink on the native lizard fauna, rather than any documented evidence for its impact (Chapple *et al.* 2016a). However, the plague skink possesses several traits associated with successful invaders. It is a flexible generalist feeder, consuming up to 17 orders of invertebrate prey within its native range (Lunney *et al.* 1989) and is found in a range of habitats, including human-disturbed habitats (Peace 2004; Chapple *et al.* 2014, 2016a). It reaches sexual maturity in one year and is relatively fecund, laying clutches of three to seven eggs in New Zealand, and sometimes multiple clutches per year (Peace 2004; Chapple *et al.* 2016a; Miller *et al.* 2017). Moreover, it is known to nest communally, with nests of up to 200 eggs (Chapple *et al.* 2014, 2016a). Finally, it is small, around 45–50 mm adult snout-vent length (SVL), with an

innocuous brown colouration (Miller *et al.* 2017). The tendency towards an r-selected life history strategy of the plague skink is in stark contrast to the slower life histories exhibited by endemic New Zealand skinks (viviparous, 2–4 years to mature, small clutch sizes (3–5); Cree & Hare 2016) suggesting it has the potential to effectively out-compete native skinks through interference or exploitation.

Here, we use a mark-recapture study to investigate the potential impact of the invasive plague skink on native skink species in northern New Zealand. Specifically, we conducted a field-based study to assess the degree of range and niche overlap between plague skinks and three native skink species. We predicted, as an invader, plague skinks would exhibit a broader ecological niche enabling them to be more abundant than native skinks. In addition, we predicted that high densities of plague skinks would suppress the population size of native skink species.

MATERIALS AND METHODS

Mark-recapture surveys

Skink surveying took place from October through November 2018 at two sites (Hill Site: 36.60164°S, 174.81702°E; Camp Site: 36.61259°S, 174.82834°E) within Shakespear Regional Park, New Zealand (Fig. 1). The study area is a peninsula containing a habitat mosaic of remnant vegetation, revegetated, and farmed land. Prior to 2009, the park had a mammal pest control programme targeting rodents, hedgehogs, mustelids, possums, cats and rabbits using a toxin bait and trapping network, as well as shooting for rabbits. Then between October 2010 and March 2011, a 1.7 km mammal exclusion ('predator-proof') fence was erected across the headland, from Army Bay to Okoromai Bay, effectively enclosing Shakespear Regional Park and the adjacent New Zealand Defence Force land (total enclosed area of 512 ha). In July and August 2011, a mammal eradication programme was carried out involving a series of aerial bait (brodifacoum) drops by helicopter and trickle baiting applied around the coastline. Pest eradication (except for mice) was achieved in December 2011. There is a network of traps and tracking tunnels, both inside the park and outside the fence, to monitor for predator incursions. Seven native lizard species, four skinks (copper skink, *Oligosoma aeneum*; ornate skink, *O. ornatum*; moko skink, *O. moco*; shore skink, *O. smithi*) and three geckos (Pacific gecko, *Dactylocnemis pacificus*; forest gecko, *Mokopirirakau granulatus*; Auckland green gecko, *Naultinus elegans*), are known to occur in Shakespear Regional Park. Species richness within the park is similar to areas outside of the reserve, but abundances of the native species are higher within the park.

Various trapping methods were deployed in a grid pattern within each site. The Hill Site had 30 pitfall traps (4 L buckets) and 12 artificial cover objects (ACOs), whereas the Camp Site sites had 29 pitfall traps and 11 ACOs. Pitfall traps were baited with tinned pear. Loose vegetation and a damp sponge were provided to prevent predation and desiccation of captured lizards, respectively. Sites were monitored twice daily (morning and afternoon sessions) for three days with the direction of movement around the site alternating for each trapping session. Opportunistic hand capture was also performed during each session. After the three consecutive survey days, traps were decommissioned, and the other field site surveyed. Alternating between sites maximised total surveying days while allowing sites to rest. Both sites were surveyed for a total of nine days (18 sessions).

For all captured lizards, species, snout-vent length (SVL), head length (HL), head width (HW), tail length (TL), tail condition (full or regenerating), sex, recapture status, identifying marks (e.g. missing toes, limbs, scarring) and GPS location (Garmin GPSmap 78s) were recorded. Each newly caught individual was given an identifying mark on its lateral side with a non-toxic marker and released at the site of capture. This mark allowed for identification of recaptured individuals but was placed so as to not attract attention from predators or be rubbed off easily on the substrate. In the case of partially obscured marks, body measurements and characteristics were used to verify individual identification.

Habitat characterisation

To assess habitat preferences of invasive and native skink species, the microhabitat within a 50 cm diameter plot surrounding each trap location was assessed in terms of vegetation structure. Traps surrounded by understories comprised primarily of remnant pastoral grasses were designated as simple, while microhabitats regenerating shrubs and vines (most notably, *Muehlenbeckia complexa*) were considered complex. Four temperature data loggers (thermometer iButtons DS1921G; Maxim Integrated, San Jose, CA, USA) were deployed in each of the Camp and Hill Sites, with two positioned in shaded areas and two in open areas. The loggers were placed on the ground, sheltered by simple vegetation, two days prior to the commencement of the field surveys. Temperature was measured every four hours during the skinks' daily activity period for the duration of the field study. However, due to data logger malfunctions, only data collected from a single temperature data logger from each of the sites was used in the analyses. Rainfall information was derived from meteorological site AccuWeather (AccuWeather Inc., State College, PA, USA).

Statistical analysis

Data were analysed using the statistical software R (R Development Core Team 2018). All data were checked for normality and homogeneity of variance using Shapiro–Wilk tests and diagnostic plots. Non-Gaussian data were analysed using non-parametric approaches. For lizards caught by hand, only those captured at trap sites were included analyses assessing abundance, species richness and habitat preferences while the analyses associated with population
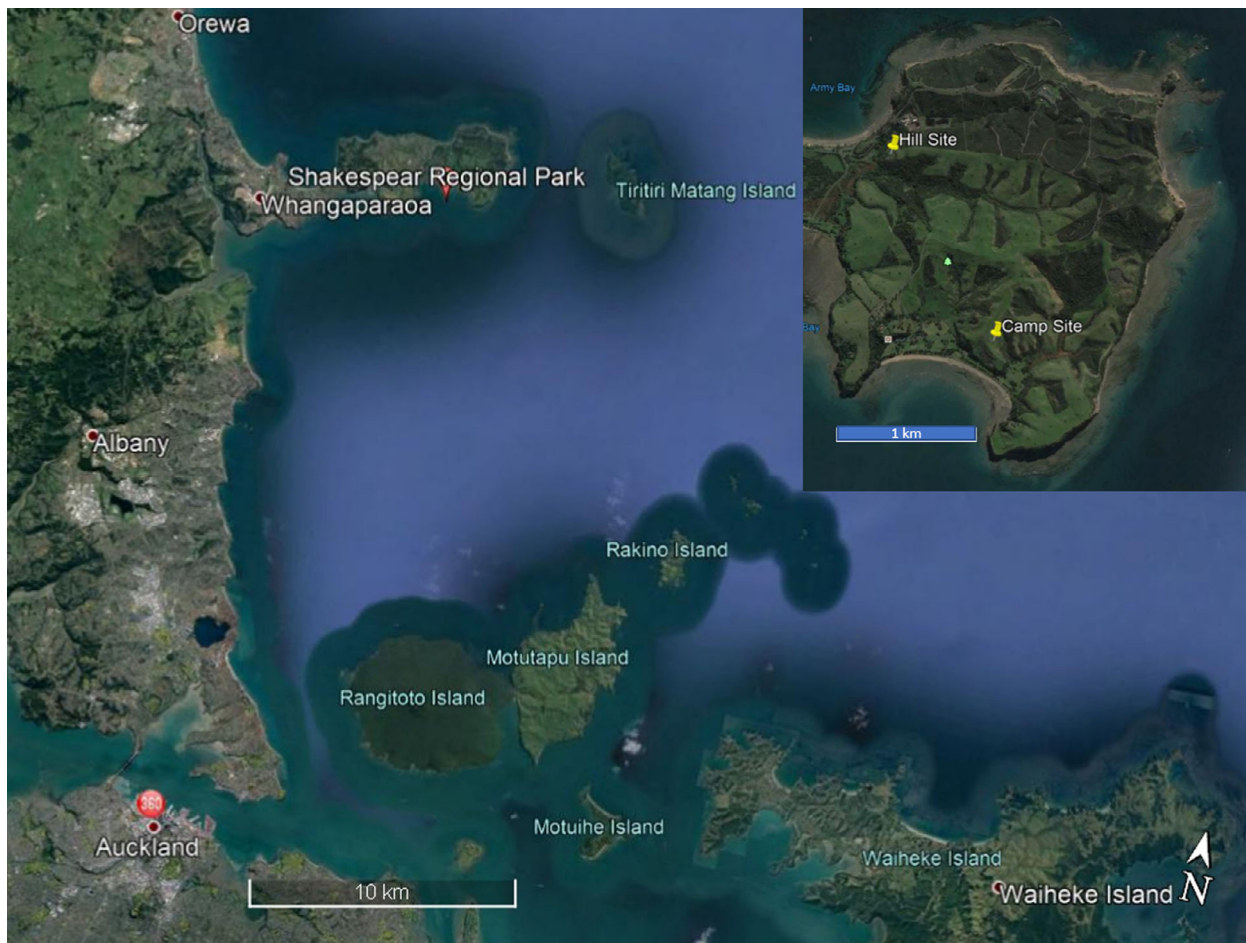
Fig. 1. Location of Shakespear Regional Park, New Zealand. Inset shows locations of the two field sites, Camp and Hill Site (Google Earth Pro 2019).

size and morphology included all lizards irrespective of capture method.

Abundance was calculated as the number of skinks of each species captured at each trap site. Variation in the measure of abundance between species, sites and habitat type was assessed using a generalised linear model (GLM) with a Poisson distribution. Abundance was included as the response variable while species, site ID and habitat complexity were included as fixed effects. Where differences between species were identified, contrasts were generated using the *lsmeans* function ('lsmeans' package) to identify which paired comparisons were significant. A GLM with Poisson distribution was then used to determine if the abundance of native species influenced the number of plague skinks. The total abundance of all native species along with site ID and habitat type were included as fixed factors. This same model structure was used to examine whether the abundance of each of the native species was influenced by the abundance of plague skink individuals; however, plague skink abundance was used as the fixed factor. The Moko skink was excluded from these analyses examining the level of influence groups of lizards (native and invasive) had on

abundance due to low capture rates which precluded comparisons to be performed.

Species richness was calculated as the number of species captured. To test for differences in richness among sites and habitat types, a GLM with Poisson distribution was used. Species richness was the response, and site ID and habitat complexity were fixed factors. Again, contrasts were generated using the *lsmeans* function to identify which paired comparisons among species were significant.

The package Rcapture (version 1.4-2; Rivest & Baillargeon 2014) was used to estimate population sizes, and associated confidence intervals, of skinks from the mark-recapture data. Due to low capture and recapture rates of copper and moko skinks, these species could not be included in the analysis. Data were analysed in the default binary matrix. A closed population was assumed as there was a relatively short survey period and open population models involve additional mathematical complexity and can exclude data. Akaike's information criterion (AIC) was used for model selection (Baillargeon & Rivest 2007; Appendix S1). Google Earth Pro (2019; version 7.3.2.5495) was used to plot polygons denoting the bounds of trap locations and capture locations of each species at

both field sites. These polygons were then used to estimate site area and range overlap of species. Variation in recapture rate between species was assessed using a linear model with species and habitat complexity as fixed effects.

Climate and vegetation structure were used to evaluate habitat preferences for each species. Environmental temperature data extracted from data loggers were used to determine the minimum, maximum and mean temperatures of both sites. Activity temperature for each individual was based on the temperature at the time of capture. A principal component analysis (PCA) with varimax rotation was applied to reduce the dimensionality of climatic data, including environmental temperatures and rainfall. All variables were scaled and centred. Two PC components were retained based on the Kaiser–Guttman criterion (eigenvalues >1) and used for further analyses. Habitat preferences for each species was assessed separately using GLMs with a Poisson error distribution. Session (morning or afternoon), climatic PCs, field temperature, site and habitat complexity were included as fixed effects and species abundance as the response variable. Site was excluded from the model assessing habitat preferences in copper skinks as this species had very low capture rates in the Camp site. Variation in habitat use between species was evaluated using GLMs using the same model structure as previously described. Where differences between species were identified, contrasts were generated using the function *lsmeans* were performed to identify which paired comparisons were significant.

To assess differences in morphological traits between species and between sites, a PCA with varimax rotation was applied to reduce the dimensionality of body (SVL, HW and HL) and tail measurements (TL). All variables were scaled and centred. Two PC components were retained based on the Kaiser–Guttman criterion (eigenvalues >1) and PC scores used for further analyses. A linear model was performed with species, site and habitat complexity included as fixed factors. Contrasts were generated ('lsmeans' package) to identify which paired comparisons were significant. The influence of species, site and habitat complexity on the frequency of tail loss between species was assessed using a GLM with binomial error distribution (yes/no).

RESULTS

Abundance and species richness

A total of 305 plague skinks (Hill = 188; Camp = 117), 78 ornate skinks (Hill = 19; Camp = 59), 41 copper skinks (Hill = 38; Camp = 3) and one moko skink (Hill Site) were captured in the course of the study (Table 1). Abundance differed between species, with plague skinks having higher abundance than all of the native skinks (copper skinks: estimate = 2.01, $Z = 12.06$, $P < 0.001$; ornate skinks: estimate = 1.36, $Z = 10.75$, $P < 0.001$; and moko skinks: estimate = 5.72, $Z = 5.71$, $P < 0.001$). Abundance did not differ between sites (estimate = 0.18, $Z = 1.56$, $P = 0.12$)

or habitat complexity (estimate = -0.05, $Z = -0.40$, d.f. = 1, $P = 0.69$). The presence of native skinks was positively associated with the abundance of plague skinks (estimate = 0.05. $Z = 2.22$, $P = 0.03$), where the number of plague skinks captured at each trap location increased with the presence of copper and ornate skinks. By contrast, the presence of plague skinks did not influence abundance of native skinks (copper skinks: estimate = -0.01, $Z = 0.51$, $P = 0.61$; ornate skinks: estimate = 0.01, $Z = 0.54$, $P = 0.59$). Species richness did not vary between sites (estimate = 0.08, $Z = 0.39$, $P = 0.70$) or habitat type (estimate = 0.08, $Z = 0.34$, $P = 0.74$).

Recapture rates between species were as follows: plague = 86, ornate = 16 and copper = 0. The rate at which individuals were recaptured was higher in plagues skinks than that of copper skinks (estimate = -21.5, $t = 3.15$, d.f. = 8, $P = 0.03$). By contrast, recapture rates did not vary between copper and ornate skinks (estimate = -4.00, $t = -0.59$, d.f. = 8, $P = 0.83$) nor did they vary as a function of habitat complexity (estimate = -3.33, $t = -0.60$, d.f. = 8, $P = 0.57$). Interestingly, unlike the plague skink, native skinks were only recaptured at the same trap location in which they were initially captured.

Results from the mark-recapture analyses indicated that plague skinks have a larger population size than ornate skinks. Plague skink populations were estimated to be 436 at the Hill Site and 1228 at the Camp Site while population size estimates for the ornate skink were 75 and 387 at the Hill and Camp Sites, respectively (Fig. 2). Based on the capture locations of plague skinks, the vast majority were always recaptured at the same trap location; however, the further distance between captures for an individual was 32.6 m. Overall, the plague skink was found to occur broadly throughout both field sites (Fig. 3). By contrast, both the ornate and copper skinks had smaller ranges, 86.6% and 13.4% of the Camp Site and 53.1% and 83.5% of the Hill Site, respectively.

Habitat characterisation

The Hill Site was composed of 80% complex and 20% simple vegetative understorey habitat structures while the habitat at the Camp Site was comprised of 70% simple and 30% complex structure. Average environmental temperatures during the daily activity period were higher at the Camp Site (mean = 19.70°C; range = 11.64–29.16°C) than the Hill Site (mean = 17.80°C; range = 12.04–28.55°C). The thermal environment differed between sites (estimate = -1.90, $t = -3.54$, d.f. = 176, $P = 0.001$). PCA analyses of climatic measures produced two axes of variation, PC1 (75% of the variation) was characterised by positive loadings of maximum and

Table 1. Summary of captured invasive and native skink species within simple and complex habitat types within Hill and Camp Sites

Species	Hill Site		Camp Site		Overall		Total
	Simple	Complex	Simple	Complex	Simple	Complex	
Plague skink	32	156	83	34	190	115	305
Copper skink	8	30	2	1	10	31	41
Ornate skink	4	15	42	17	46	32	78
Moko skink	0	1	0	0	0	1	1
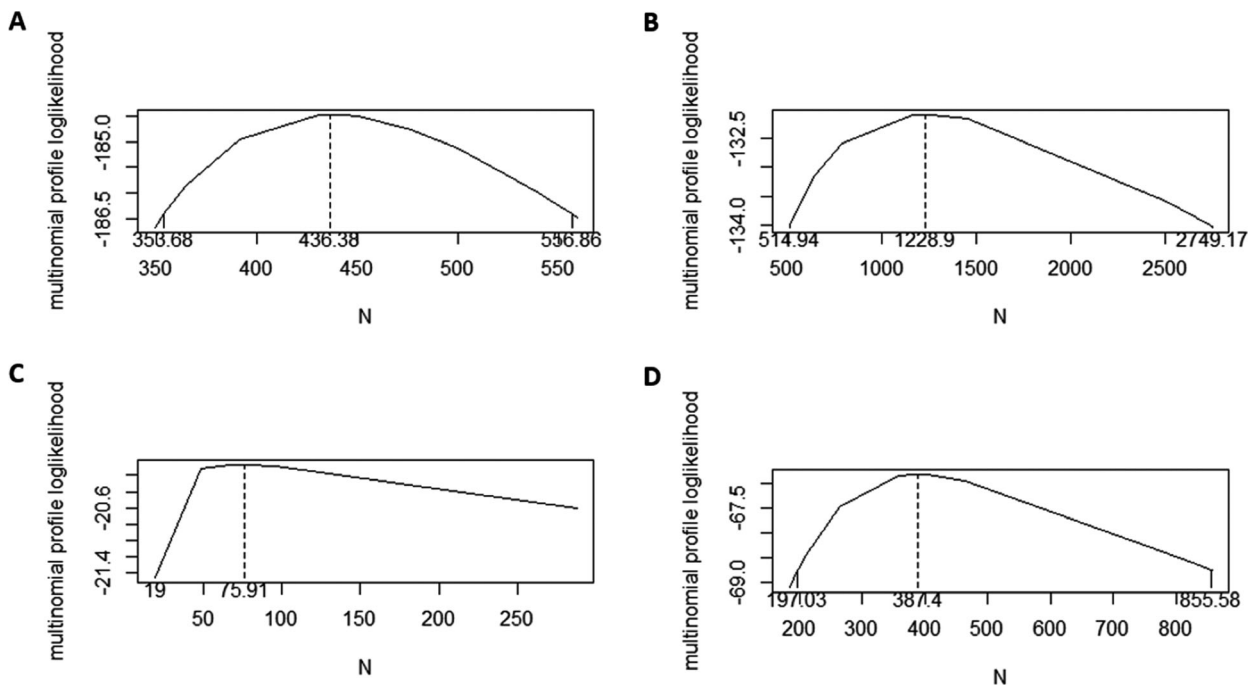
Fig. 2. Profile likelihood confidence interval plots for skink populations at Shakespear Regional Park, New Zealand. (a) Plague skink population estimate at the Hill Site, (b) plague skink population estimate at the Camp Site, (c) ornate skink population estimate at the Hill Site, (d) ornate skink population estimate at the Camp Site. The peak indicates the most probable population estimate. 95% confidence interval bounds are denoted by vertical lines.

mean temperature and negative loadings of minimum temperature while rainfall had strong negative loadings for PC2 (25% of the variation). Habitat preferences differed between species, with plague skinks occurring more often in complex habitats with higher field temperatures than native species (copper: estimate = 2.61, $Z = 16.87$, $P < 0.001$; moko: estimate = 4.80, $Z = 10.70$, $P < 0.001$ ornate: estimate = 1.92, $Z = 16.95$, $P < 0.001$). Indeed, native skinks were observed to be more prone to heat (e.g. dehydration in warm weather) and handling stress than the plague skink (observed both in the field, and in temporary housing). The propensity of native skinks to react more strongly to stressors was corroborated by anecdotal evidence from other researchers (David Craddock, pers. comm.). When considering each species separately, plague skinks

preferred complex vegetation structure with high field temperatures (Table 2). However, despite having a preference for high thermal environments, this species demonstrated greater levels of activity during the cooler morning hours than during the afternoon. Yet, neither environmental temperature nor rainfall influenced use of habitat by the plague skink. None of the ecological variables were found to be influential in habitat use of the ornate or copper skink (Table 2).

Morphology

Summary of skink morphometrics by species and site is presented in Table 3. PCA analyses on morphometric data generated two principle components. Morph PC1 (58% of the variation) described skinks
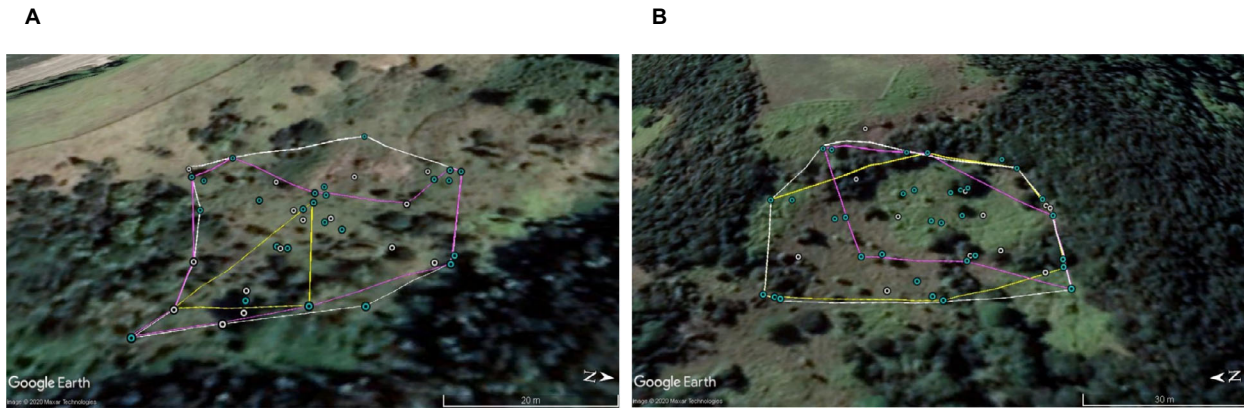
Fig. 3. Polygons denoting bounds of trap locations and skink capture locations at (a) Camp Site and (b) Hill Site. Yellow lines denote the boundary of trap locations and plague skink range, pink lines the boundary of ornate skink range, white the boundary of copper skink range. Image modified from Google Earth Pro (2019).

Table 2. Results of the generalised linear models testing the effects of climatic and structural variables on habitat preferences of invasive and native skink species

Species	Parameter	Estimate	SE	Z	P
Plague skink	Time: morning	0.32	0.09	3.70	**<0.001**
	Climate PC1	3.88E + 08	2.80E + 08	1.38	0.17
	Climate PC2	1.64E + 07	1.19E + 07	1.38	0.17
	Field temp	−0.07	0.02	−4.66	**<0.001**
	Site: Hill	1.34E + 09	9.65E + 08	1.38	0.17
	Habitat type: simple	−0.57	0.09	−6.73	**<0.001**
Copper skink	Time: morning	0.41	0.36	1.14	0.26
	Climate PC1	0.15	0.12	1.19	0.23
	Climate PC2	0.22	0.23	0.95	0.34
	Field temp	−0.01	0.09	−0.12	0.91
	Habitat type: simple	−0.66	0.38	−1.73	0.08
Ornate skink	Time: morning	−0.05	0.24	−0.21	0.84
	Climate PC1	6.09E + 08	5.30E + 08	1.15	0.25
	Climate PC2	−6.63E + 07	5.76E + 07	−1.15	0.25
	Field temp	−0.05	0.04	−1.29	0.20
	Site: Hill	−2.18E + 09	1.90E + 09	−1.15	0.25
	Habitat type: simple	−0.05	0.21	−0.25	0.81

Climate PC1 is characterised by positive loadings of minimum, maximum and mean environmental temperatures whereas climate PC2 is characterised by negative loadings of rainfall. Habitat type denotes either simple or complex understory vegetation structure. Bold indicates statistically significant P-values.

as having positive loadings for SVL, HW and HL while morph PC2 (22% of the variation) was characterised by TL. Morphological traits varied among species for both morph PC1 (plague: estimate = −1.43, $t = -6.21$, d.f. = 507, $P < 0.001$; moko: estimate = 2.58, $t = 2.53$, d.f. = 507, $P = 0.02$; ornate: estimate = −0.23, $t = -0.83$, d.f. = 507, $P = 0.41$) and morph PC2plague: estimate = 0.53, $t = 3.60$, d.f. = 507, $P < 0.001$, moko = estimate = 0.36, $t = 0.56$, d.f. = 507, $P = 0.57$, ornate: estimate = 0.29, $t = 1.64$, d.f. = 507, $P = 0.10$). Plague skinks had shorter body and head lengths as well as narrower heads than native skinks (copper: estimate = 1.43, $t = -6.21$, d.f. = 507, $P < 0.001$; ornate: estimate = −1.20, $t = -6.57$, d.f. = 507, $P < 0.001$; moko: estimate = −4.01, $t = -4.01$, d.f. = 507, $P < 0.001$). Moko skinks had larger body and head proportions than ornate skinks (estimate = 2.81, $t = 2.77$, d.f. = 507, $P = 0.03$) but did not differ with copper skinks (estimate = −2.58, $t = 2.53$, $P = 0.06$). Within species, the body and head proportions were similar between sites (estimate = −0.17, $t = -1.17$, d.f. = 507, $P = 0.24$) and was not influenced by

Table 3.   Summary of skink morphometric measures and frequency of full and regenerated tails for each species and site

Species	Site	N	SVL (mm) Mean	Min	Max	Tail length (mm) Mean (SE)	Min	Max	Head width (mm) Mean (SE)	Min	Max	Head length (mm) Mean (SE)	Min	Max	# Full tails	# Regen- erated tails
Plague	Camp	184	42.03 ± 0.96	13.10	77.60	38.02 ± 1.04	5.00	64.20	5.81 ± 0.10	2.00	11.10	8.72 ± 0.14	3.10	13.00	46	138
	Hill	234	37.59 ± 0.34	24.20	46.10	43.66 ± 0.88	3.90	74.00	5.41 ± 0.04	3.60	6.80	8.05 ± 0.06	5.00	10.00	54	180
Copper	Camp	3	56.80 ± 10.64	30.80	71.50	38.37 ± 8.11	20.00	54.10	7.03 ± 0.83	5.00	8.10	10.77 ± 1.40	7.40	13.00	1	2
	Hill	40	51.02 ± 0.96	33.00	60.90	43.38 ± 1.64	9.90	60.90	6.27 ± 0.09	5.00	7.00	9.52 ± 0.12	6.80	13.00	12	28
Moko	Camp	0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Hill	1	72.00 ± 0.00	72.00	72.00	58.40 ± 0.00	58.40	58.40	8.00 ± 0.00	8.00	8.00	14.20 ±	14.20	14.20	0	1
Ornate	Camp	52	46.46 ± 2.04	22.50	71.50	38.55 ± 1.87	13.00	64.90	6.25 ± 0.21	2.90	10.00	9.25 ± 0.30	5.20	13.10	15	37
	Hill	25	58.10 ± 1.30	42.00	71.00	46.97 ± 1.58	19.50	58.90	7.52 ± 0.17	6.30	9.60	10.64 ± 0.25	6.40	12.00	5	20

habitat complexity (estimate = −0.10, $t = -0.68$, d.f. = 507, $P = 0.50$). Tail length, on the other hand, was found to only differ between plague and copper skinks, with copper skinks having shorter tails (estimate = −0.53, $t = -3.60$, d.f. = 507, $P = 0.002$). However, tail length overall did vary between sites (estimate = 0.45, $t = 4.79$, d.f. = 507, $P < 0.001$). Skinks had shorter tails at the Camp Site than the Hill Site. The frequency of tail loss did not vary between species (plague: estimate = 0.40, $Z = 1.10$, $P = 0.27$; ornate: estimate = 0.35, $Z = 0.78$, $P = 0.43$), habitat types (estimate = 0.31, $Z = 1.27$, $P = 0.20$) or site ($Z = -1.30$, $P = 0.19$; Table 3).

DISCUSSION

While our study does not provide definitive evidence for competition between the plague skink and native skink species in New Zealand, we clearly demonstrate the presence of the core components required for exploitative competition to occur. Specifically, our study shows that the plague skink and native species substantially overlap in their fine-scale distribution and microhabitat use, with the plague skink substantially more abundant and widespread within both study sites. Although plague skinks are shorter and slimmer than the native skink species, with a smaller gape size, it is likely that the species overlap substantially in their insectivorous diet. Here, we discuss the potential for the plague skink to negatively impact the native skink species through exploitative competition.

As predicted, both the absolute capture rates and estimated population size of the plague skink were significantly higher than the three native skink species. Examination of the capture locations indicates that almost the entirety of both sites represents suitable habitat for the plague skink, and opportunistic sightings indicated Plague skinks were found East of the site delineation at the Hill Site, showing habitat was still suitable, despite not being captured in traps there. Indeed, the plague skink is known to be numerically dominant across a range of habitats

throughout its native Australian range (Pearce & Ferrier 2001; Taylor & Fox 2001a,b; Kanowski et al. 2006), as well as within its invasive range in Hawaii (Baker 1979), Lord Howe Island (Chapple et al. 2016b), and New Zealand (Wairepo 2018). Our results are consistent with a recent study on Great Barrier Island, New Zealand, which found the plague skink to be substantially more abundant than the same native skink species surveyed in our study (Wairepo 2018). Interestingly, although the plague skink only established and spread through the Auckland region in the 1960s–1970s (Chapple et al. 2013a; Chapple et al. 2016a), it is already the most widespread and abundant skink species in Shakespear Regional Park. Indeed, it is even likely that our population size estimates for the plague skink are underestimates, as Wairepo (2018) found trap densities of 2 m were not sufficient to eradicate the plague skink on Great Barrier Island. At our study sites, the plague skink had a higher abundance in locations where native copper and ornate skinks occurred, which enhances the potential for exploitative competition by the plague skink.

In contrast, the capture rates and estimated population sizes of the native skink species were substantially lower. Only a single moko skink was caught during the study. This is consistent with previous work, as the moko skink is a relictual species on the mainland North Island (van Winkel et al. 2018; Hare et al. 2016; Chapple & Hitchmough 2016). The ornate and copper skinks were more common at our study sites, with copper skink the dominant native species at the Hill Site and found more widely throughout this site. Nationally, copper skink is one of the most common and widespread native skink species in New Zealand (van Winkel et al. 2018; Chapple 2016). The ornate skink was the most abundant native species at the Camp Site. Although ornate skink is listed as Least Concern on the IUCN Red List (Hitchmough et al. 2019), its populations are declining, and it is considered conservation dependent (Hitchmough et al. 2016b). However, it is clear from our study that it can reach high abundances under favourable conditions, even in the presence of the high-density plague skink populations.

Interestingly, there was no evidence that the plague skink competitively excludes the ornate or copper skink, as the abundance of these native species at trap locations was not found to be influenced by the presence of plague skink.

The relatively high abundances of the plague skink, compared with the native skink species, could be explained by various aspects of their ecology and physiology. The plague skink is a generalist species, with the capacity to feed upon a wide variety of invertebrates (Lunney *et al.* 1989) and succeed in a range of habitats (Baker 1979; Peace 2004; Chapple *et al.* 2014, 2016a). This may explain why, as predicted, the plague skink had a broader distribution within each study site and was more abundant across both study sites and all microhabitat types. Although both native species are generalist insectivores (Porter 1987; Hare *et al.* 2016), they have larger body sizes compared to the plague skink. General ecological theory suggests that smaller species, such as the plague skink will be found at higher abundances than larger species (Peters & Wassenberg 1983; Peters & Raelson 1984), such as the native skink species. These effects could be further intensified by the disparate reproductive strategies of these species. The plague skink is oviparous lays clutches of three to seven eggs in New Zealand, and can lay multiple clutches her season (Peace 2004; Chapple *et al.* 2016a). In contrast, the native species are viviparous (Cree 1994; Cree & Hare 2016), a reproductive strategy often associated with reduced fecundity (Angelini & Ghiara 1984; Cree 1994; Cree & Hare 2016). The ornate skink produces on average five young annually (Cree & Hare 2016), and female copper skinks average only 2.6 young per year (Habgood 2003). Moreover, differences in densities may also be attributed to their divergent social behaviours; the plague skink is known to be communal (e.g. Chapple *et al.* 2011, 2016b), whereas ornate skinks are aggressive and territorial, and copper skinks can eat smaller conspecifics (van Winkel *et al.* 2018).

Both the head widths and head lengths of the plague skink were significantly smaller than the co-occurring native species. This could potentially influence the diet of each skink species. In species that swallow their prey whole, such as in insectivorous lizards, gape size can limit the consumption of larger prey (DeMarco *et al.* 1985; Schael *et al.* 1991; Lima *et al.* 2000). Gape can be limiting not only as a result of aperture size, but because larger jaws can have greater musculature, enabling jaws to close faster and harder than smaller individuals (Meyers *et al.* 2002). Jaw strength is likely to limit the predation of harder-bodied prey, such as coleopterans and orthopterans, whereas gape size likely limits the size of softer-bodied prey (Porter 1987). However, stomach and faecal samples from these skinks are consistent, to an extent, with the patterns predicted from gape data. Harder-bodied coleopterans are more commonly eaten by ornate skinks, followed by copper skinks and then delicate skinks (Porter 1987; Toft 2012). This corresponds with the assumption that a larger gape is accompanied by greater jaw strength and ability to consume harder-bodied prey (Porter 1987). Furthermore, large prey, such as caterpillars, were frequently consumed by ornate skinks, but completely absent from plague skink specimens (Toft 2012). In laboratory-based food preference trials, small (5 mm) and medium (10 mm) crickets were significantly preferred over large (15 mm) crickets, and while plague skinks could successfully subdue and consume large crickets, they had a lower success rate (our unpublished data). Yet, there is still substantial overlap in the diet of the plague skink and native species, with the prey size of all species found to be primarily less than 6 mm (Porter 1987; Toft 2012). There may also be some degree of differentiation among the activity times of these species. Plague skinks are considered to be diurnal, and this was further substantiated by its greater preference for surface activity in the morning surveys. By contrast, copper skinks, while predominantly diurnal, may be crepuscular, and ornate skinks are predominantly crepuscular (van Winkel *et al.* 2018). Indeed, we found no differences in the capture rates of the native species between the morning and afternoon sessions. Temporal partitioning of foraging may facilitate co-existence of potential competitors and prevent exclusion of native species (Richards 2002; Kronfeld-Schor & Dayan 2003). However, both the degree of both dietary and temporal overlap indicates the potential for exploitative and interference competition to occur between the plague skink and native New Zealand skink species.

CONCLUSIONS AND FUTURE RESEARCH

While we have demonstrated the potential for competition, most likely exploitative, between the plague skink and native New Zealand skink species, further field- and laboratory-based studies and experiments are required to confirm the presence of such competition. An ideal study location to investigate the existence of exploitative competition is Great Barrier Island. The plague skink was inadvertently introduced to the island in 2013 and is currently spreading across Great Barrier Island (Wairepo 2018). Thus, within a small geographic region, it would be possible to compare the ecology, life history and reproduction of native skink species within regions with, and without, plague skink species. Such a long-term study would provide more definitive evidence for the existence of

exploitative competition. Similarly, laboratory-based trials could be used to determine whether there is interference competition between plague skinks and native skink species. For instance, Downes and Bauwens (2002) using basking site competition trials to demonstrate that invasive Italian wall lizards (*Podarcis sicula*) excluded native Dalmation wall lizards (*P. melisellensis*) from basking sites, resulting in decreased growth rates in the native species. Thus, such studies will provide a clearer picture as to whether the plague skink has negative impacts on the native skink fauna in New Zealand.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

AUTHOR CONTRIBUTIONS

Jaclyn Harris: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing-original draft (equal). **Chelsea Smith:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing-original draft (equal). **Dylan van Winkel:** Conceptualization (equal); Methodology (equal); Writing-review & editing (equal). **Dianne Brunton:** Conceptualization (equal); Supervision (equal); Writing-review & editing (equal). **Celine Goulet:** Conceptualization (equal); Formal analysis (equal); Methodology (equal); Supervision (equal); Writing-original draft (equal). **David G. Chapple:** Conceptualization (equal); Supervision (equal); Writing-original draft (equal).

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Data availability statement

All data will be deposited in FigShare upon acceptance of the manuscript.

REFERENCES

Angelini F. & Ghiara G. (1984) Reproductive modes and strategies in vertebrate evolution. *Ital. J. Zool.* **51,** 121–203.

Baillargeon S. & Rivest L.-P. (2007) Rcapture: loglinear models for capture-recapture in R. *J. Stat. Softw.* **19,** 1–31.

Baker J. K. (1979) The rainbow skink, *Lampropholis delicata*, in Hawaii. *Pac. Sci.* **33,** 207–12.

Blackburn T. M., Cassey P., Duncan R. P., Evans K. L. & Gaston K. J. (2004) Avian extinction and mammalian introductions on oceanic islands. *Science* **305,** 1955–8.

Blackburn T. M., Lockwood J. L. & Cassey P. (2009) *Avian Invasions: The Ecology and Evolution of Exotic Birds*. Oxford University Press, Oxford.

Blackburn, T. S., Pysek, P. & Bacher, S. *et al.* (2011) A proposed unified framework for biological invasions. *Trends. Ecol. Evol.* **26,** 333–339.

Campbell E. W. (1996) The effect of brown tree snake (*Boiga irregularis*) predation on the island of Guam's extant lizard assemblages. Unpublished PhD thesis, Ohio State University. [Cited 30 November 2020]. Available from URL: https://etd.ohiolink.edu/!etd.send_file?accession=osu1487933648648261&disposition=inline.

Chapple D. G. (2016) *New Zealand Lizards*, 381p. Springer, Cham, Switzerland. https://doi.org/10.1007/978-3-319-41674-8.

Chapple D. G. & Hitchmough R. A. (2016) Biogeography of New Zealand lizards. Chapter 5. In: *New Zealand Lizards* (ed D. G. Chapple) pp. 109–31. Springer, Cham, Switzerland. https://doi.org/10.1007/978-3-319-41674-8_5.

Chapple D. G., Knegtmans J., Kikillus H. & van Winkel D. (2016a) Biosecurity of exotic reptiles and amphibians in New Zealand: building upon Tony Whitaker's legacy. *J. R. Soc. N. Z.* **46,** 66–84.

Chapple D. G., Miller K. A., Chaplin K., Barnett L., Thompson M. B. & Bray R. D. (2014) Biology of the invasive delicate skink (*Lampropholis delicata*) on Lord Howe Island. *Aust. J. Zool.* **62,** 498–506.

Chapple D. G., Miller K. A., Kraus F. & Thompson M. B. (2013a) Divergent introduction histories among invasive populations of the delicate skink (*Lampropholis delicata*): has the importance of genetic admixture in the success of biological invasions been overemphasized? *Divers. Distrib.* **19,** 134–46.

Chapple D. G., Reardon J. T. & Peace J. E. (2016b) Origin, spread and biology of the invasive plague skink (*Lampropholis delicata*) in New Zealand. Chapter 13. In: *New Zealand Lizards* (ed D. G. Chapple) pp. 341–59. Springer, Cham, Switzerland.

Chapple D. G., Simmonds S. M. & Wong B. B. M. (2011) Know when to run, know when to hide: can behavioral differences explain the divergent invasion success of two sympatric lizards? *Ecol. Evol.* **1,** 278–89.

Chapple, D. G., Simmonds, S. M. & Wong, B. B. M. (2012) Can behavioral and personality traits influence the success

of unintentional species introductions?. *Trends. Ecol. Evol.* **27,** 57–64.

Chapple D. G., Whitaker A. H., Chapple S. N. J., Miller K. A. & Thompson M. B. (2013b) Biosecurity interceptions of an invasive lizard: origin of stowaways and human-assisted spread within New Zealand. *Evol. Appl.* **6,** 324–39.

Cole N. C., Jones C. G. & Harris S. (2005) The need for enemy-free space: the impact of an invasive gecko on island endemics. *Biol. Cons.* **125,** 467–74.

Cree A. (1994) Low annual reproductive output in female reptiles from New Zealand. *N. Zeal. J. Zool.* **21,** 351–72.

Cree A. & Hare K. M. (2016) Reproduction and life history of New Zealand lizards. Chapter 7. In: *New Zealand Lizards* (ed D. G. Chapple) pp. 169–206. Springer, Cham.

David P., Thebault E., Anneville O., Duyck P.-F., Chapuis E. & Loeuille N. (2017) Impacts of invasive species on food webs: a review of empirical data. In *Networks of Invasion: A Synthesis of Concepts*, Vol. 56 (eds D. A. Bohan, A. J. Dumbrell & F. Massol) pp. 1–60. Elsevier, Cham.

DeMarco V. G., Drenner R. W. & Ferguson G. W. (1985) Maximum prey size of an insectivorous lizard, *Sceloporus undulatus garmani*. *Copeia* **1985,** 1077–80.

Doherty T. S., Glen A. S., Nimmo D. G., Ritchie E. G. & Dickman C. R. (2016) Invasive predators and global biodiversity loss. *PNAS* **113,** 11261–5.

Downes S. J. & Bauwens D. (2002) An experimental demonstration of direct behavioral interference in two Mediterranean lizard species. *Anim. Behav.* **63,** 1037–46.

Fisher R. & Ineich I. (2012) Cryptic extinction of a common Pacific lizard *Emoia impar* (Squamata, Scincidae) from the Hawaiian Islands. *Oryx* **46,** 187–95.

Google Earth Pro. (2019). [Cited 30 November 2020]. Available from URL: https://www.google.com/earth/

Habgood M. J. (2003) Behavioural interactions between copper (*Cyclodina aenea*) and moko (*Oligosoma moco*) skinks: implications for translocations. Unpublished MSc thesis, University of Auckland, New Zealand.

Hare K. M., Chapple D. G., Towns D. R. & van Winkel D. (2016) The ecology of New Zealand's lizards. Chapter 6. In: *New Zealand Lizards* (ed D. G. Chapple) pp. 133–68. Springer, Cham. https://doi.org/10.1007/978-3-319-41674-8_6

Hare K. M., Daugherty C. H. & Chapple D. G. (2008) Comparative phylogeography of three skink species (*Oligosoma moco, O. smithi, O. suteri*; Reptilia: Scincidae) in northeastern New Zealand. *Mol. Phylogenet. Evol.* **46,** 303–15.

Hitchmough R. A., Barr B., Lettink M. *et al.* (2016a) *Conservation Status of New Zealand Reptiles, 2015. New Zealand Threat Classification Series 17.* Department of Conservation, Wellington.

Hitchmough R. A., Patterson G. B. & Chapple D. G. (2016b) Putting a name to diversity: taxonomy of the New Zealand lizard fauna. Chapter 4. In: *New Zealand Lizards* (ed D. G. Chapple) pp. 87–108. Springer, Cham.

Hitchmough R., van Winkel D. & Lettink M. (2019) *Oligosoma ornatum*. The IUCN Red List of Threatened Species 2019: e.T120189934A120192644. [Cited 05 May 2020.] https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T120189934A120192644.en.

Human K. G. & Gordon D. M. (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* **105,** 405–12.

Hunsaker D. I. & Breese P. (1967) Herpetofauna of the Hawaiian islands. *Pac. Sci.* **21,** 423–8.

Kanowski J. J., Reis T. M., Catterall C. P. & Piper S. D. (2006) Factors affecting the use of reforested sites by reptiles in cleared rainforest landscapes in tropical and subtropical Australia. *Restor. Ecol.* **14,** 67–76.

Kraus F. (2009) *Alien Reptiles and Amphibians: A Scientific Compendium and Analysis.* Springer Science & Business Media, Amsterdam.

Kraus F. (2015) Impacts from invasive reptiles and amphibians. *Annu. Rev. Ecol. Evol. Syst.* **46,** 75–97.

Kronfeld-Schor N. & Dayan T. (2003) Partitioning of time as an ecological resource. *Annu. Rev. Ecol. Evol. Syst.* **34,** 153–81.

Kupferberg S. J. (1997) Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. *Ecology* **78,** 1736–51.

Lever C. (2003) *Naturalized Reptiles and Amphibians of the World.* Oxford University Press, Oxford and New York.

Lima A. P., Magnusson W. E. & Williams D. G. (2000) Differences in diet among frogs and lizards coexisting in subtropical forests of Australia. *J. Herpetol.* **34,** 40–6.

Lunney D., Ashby E., Grigg J. & Oconnell M. (1989) Diets of Scincid Lizards *Lampropholis guichenoti* (Dumeril and Bibron) and *Lampropholis delicata* (De Vis) in Mumbulla State Forest on the South Coast of New-South-Wales. *Aust. Wildl. Res.* **16,** 307–12.

Mack R. N., Simberloff D., Mark Lonsdale W., Evans H., Clout M. & Bazzaz F. A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10,** 689–710.

McGeoch M. A., Butchart S. H., Spear D. *et al.* (2010) Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. *Divers. Distrib.* **16,** 95–108.

Meyers J. J., Herrel A. & Birch J. (2002) Scaling of morphology, bite force and feeding kinematics in an iguanian and a scleroglossan lizard. In: *Topics in Functional and Ecological Vertebrate Morphology* (eds P. Aerts, K. D'Août, A. Herrel & R. Van Damme), pp. 47–62. Shaker Publishing, Maastricht, Netherlands.

Miller K. A., Duran A., Melville J., Thompson M. B. & Chapple D. G. (2017) Sex-specific shifts in morphology and colour pattern polymorphism during range expansion of an invasive lizard. *J. Biogeogr.* **44,** 2778–88.

Moule H., Chaplin K., Bray R. D., Miller K. A., Thompson M. B. & Chapple D. G. (2015) A matter of time: temporal variation in the introduction history and population genetic structuring of an invasive lizard. *Curr. Zool.* **61,** 456–64.

Murphy B. P., Woolley L. A., Geyle H. M. *et al.* (2019) Introduced cats (*Felis catus*) eating a continental fauna: the number of mammals killed in Australia. *Biol. Cons.* **237,** 28–40.

Peace J. E. (2004) Distribution, habitat use, breeding and behavioural ecology of rainbow skinks (*Lampropholis delicata*) in New Zealand. Unpublished thesis, University of Auckland New Zealand. [Cited 30 November 2020]. Available from URL: https://www.massey.ac.nz/~mbaling/PeaceJ/Peace_MScThesis.pdf.

Pearce J. & Ferrier S. (2001) The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biol. Cons.* **98,** 33–43.

Peters R. H. & Raelson J. V. (1984) Relations between individual size and mammalian population density. *Am. Nat.* **124,** 498–517.

Peters R. H. & Wassenberg K. (1983) The effect of body size on animal abundance. *Oecologia* **60,** 89–96.

Petren K. & Case T. J. (1996) An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* **77,** 118–32.

Porter R. (1987) An ecological comparison of two *Cyclodina* skinks (Reptilia: Lacertilia) in Auckland, New Zealand. *N. Zeal. J. Zool.* **14,** 493–507.

R Core Team (2018) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Version 3.5.1. https://www.R-project.org/

Reitz S. R. & Trumble J. T. (2002) Competitive displacement among insects and arachnids. *Annu. Rev. Entomol.* **47,** 435–65.

Richards S. A. (2002) Temporal partitioning and aggression among foragers: modelling the effects of stochasticity and individual state. *Behav. Ecol.* **13,** 427–38.

Rivest L. P. & Baillargeon S. (2014) Rcapture: loglinear models for capture-recapture experiments. Version 1.4-2. [Cited 30 November 2020]. Available from URL: https://CRAN.R-project.org/package=Rcapture.

Schael D. M., Rudstam L. G. & Post J. R. (1991) Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). *Can. J. Fish. Aquat. Sci.* **48,** 1919–25.

Taylor J. E. & Fox B. J. (2001a) Assessing the disturbance impact on vegetation and lizard communities of fluoride pollution interacting with fire and mining in eastern Australia. *Austral Ecol.* **26,** 321–37.

Taylor J. E. & Fox B. J. (2001b) Disturbance effects from fire and mining produce different lizard communities in eastern Australian forests. *Austral Ecol.* **26,** 193–204.

Tingley R., Thompson M. B., Hartley S. & Chapple D. G. (2016) Patterns of niche filling and expansion across the invaded ranges of an Australian lizard. *Ecography* **39,** 270–80.

Toft R. (2012) *Summarised Results of Skink Stomach Analysis*. Entecol, Nelson.

Towns D. R., Atkinson I. A. E. & Daugherty C. H. (2006) Have the harmful effects of introduced rats on islands been exaggerated? *Biol. Invasions* **8,** 863–91.

Wairepo J. (2015) Developing biosecurity strategies for an invasive reptile, the plague skink (*Lampropholis delicata*) on Great Barrier Island. Unpublished MSc thesis, Massey University, New Zealand. [Cited 30 November 2020].Available from URL: https://mro.massey.ac.nz/handle/10179/7562.

van Winkel D., Baling M. & Hitchmough R. (2018) *Reptiles and Amphibians of New Zealand: A Field Guide*. Auckland University Press, Auckland.

Wisz M. S., Pottier J., Kissling W. D. *et al.* (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol. Rev.* **88,** 15–30.

Woinarski J. C. Z., Legge S. M., Woolley L. A. *et al.* (2020) Predation by introduced cats *Felis catus* on Australian frogs: compilation of species records and estimation of numbers killed. *Wildl. Res.* **47,** 580–588. https://doi.org/10.1071/WR19182

Woinarski J. C. Z., Murphy B. P., Legge S. M. *et al.* (2017) How many birds are killed by cats in Australia? *Biol. Cons.* **214,** 76–87.

Woinarski J. C. Z., Murphy B. P., Palmer R. *et al.* (2018) How many reptiles are killed by cats in Australia? *Wildl. Res.* **45,** 247–66.

SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Summary of model selection data used to determine the model used for the mark-recapture population estimates.