





Rapid gain and loss of predator recognition by an evolutionarily naïve lizard

HANNAH B. CLIFF,^{1,†}  MENNA E. JONES,¹  CHRIS N. JOHNSON,¹ 
 ROGER P. PECH,² BART T. BIEMANS,^{3,‡} LEON A. BARMUTA¹  AND
 GRANT L. NORBURY^{4,*} 

¹*School of Natural Sciences, University of Tasmania, Hobart, Tasmania, Australia;* ²*Manaaki Whenua – Landcare Research, PO Box 69040, Lincoln, 7640, New Zealand;* ³*Wageningen University and Research, Wageningen, The Netherlands;* and ⁴*Manaaki Whenua – Landcare Research, PO Box 176, Alexandra, 9340, New Zealand (Email: norbury@landcareresearch.co.nz)*

ABSTRACT The introduction of mammalian predators often results in loss of native biodiversity due to naiveté of native prey to novel predators. In New Zealand, an island system with virtually no native mammalian predators, introduced mammalian predators threaten a large proportion of the native fauna. A critical step in adapting to introduced predators is the ability to recognize and respond to a novel predation threat. Whether New Zealand’s lizards can do this has received little attention. We compared the basking behaviour of native McCann’s skinks (*Oligosoma maccanni*) when exposed to a live cat (*Felis catus*), cat body odour, a model raptor (representing a coevolved predator) or procedural controls. We inferred predator recognition from reductions in individual basking and higher selection for basking sites with greater refuge availability. We tested these behavioural responses for two skink populations: one from an area with high abundance of mammalian predators including feral cats and the other from a fenced conservation reserve where predators have been excluded for over 10 years (3–4 skink generations). Skinks from the high-predator population reduced basking when exposed to cat and raptor cues, whereas skinks from the predator-free population did not. These results suggest that within approximately 150 years of exposure to novel predators, McCann’s skinks might be able to recognize the threat posed by invasive mammals. However, they also demonstrate that predator recognition and antipredator behaviours may not necessarily be retained once gained. The rapid loss of basking-related antipredator behaviours might reflect the high fitness costs of reduced basking for this species. Our results indicate that the behavioural response of skinks is flexible and that skinks may maximize individual fitness by balancing the risk of predation with the costs of antipredator behaviours.

Key words: antipredator, conservation fencing, invasive predator, lizard, New Zealand.

INTRODUCTION

Introduced predators have disproportionate impacts on native prey (Salo *et al.* 2007) and are a major threat to biodiversity globally (Doherty *et al.* 2016). The impacts of introduced predators are especially clear for island systems and are generally attributed to prey naiveté, whereby prey fail to mount effective antipredator responses (Banks and Dickman 2007; Carthey and Banks 2014; Cox and Lima 2006; Sih *et al.* 2010). However, prey naiveté is dynamic, and given sufficient experience of predators, prey populations can acquire responses that may allow them to coexist with once-novel predators (Carthey and

Blumstein 2018). The first step in overcoming naiveté is recognizing novel predators as a threat (Level 1 naiveté *sensu* Banks and Dickman 2007), as this is necessary for prey to mount an effective response (Lima and Dill 1990). Predator recognition can be assessed by testing the ability of prey to discriminate a predator cue from a non-predator cue.

A number of factors influence the likelihood that a prey species will recognize a novel predation threat, some of which depend on prey species’ experience with predators over evolutionary and ecological time scales (Carthey and Blumstein 2018). For example, the ‘predator archetype hypothesis’ predicts that experience with a morphologically or behaviourally similar predator (an ‘archetype’) can prompt recognition of an introduced predator (Cox and Lima 2006). This mechanism can explain how an insular population of tamar wallabies (*Macropus eugenii*), which had never encountered a fox (*Vulpes vulpes*), initiated an antipredator response when confronted with a fox model for the first time, given their evolutionary

*Corresponding author.

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[†]Indigenous Desert Alliance, 587 Newcastle St, West Perth, Western Australia, 6005, Australia

[‡]Arcadis Nederland B.V., 5223 LL, s-Hertogenbosch, The Netherlands

experience with marsupial thylacines (*Thylacinus cynocephalus*) and recent exposure to cats (*Felis catus*) and dogs (*Canis lupus*) (Blumstein *et al.* 2000).

The length of time since introduction of a novel predator will also influence prey naiveté because predator recognition can develop via ‘rapid change’ mechanisms including plasticity, learning and rapid evolution (Carthey and Blumstein 2018). The rate at which antipredator behaviours develop depends on factors including the intensity of predation, the type of predator cue (e.g. visual/olfactory/auditory), the fitness costs associated with expression of antipredator traits, the heritability of specific antipredator traits and their genetic architecture, and the cognitive capacity of prey (Sih *et al.* 2010; Strauss *et al.* 2006). This complexity limits current predictions on acquisition of predator recognition. Information on this is particularly relevant for threatened fauna, as it is only through understanding predator recognition capabilities, as well as the potential mechanisms involved, that we can obtain a conservation prognosis for species in the presence of current and future predator threats (Carthey and Blumstein 2018).

More than 80% of New Zealand’s native lizard species listed under the New Zealand Threat Classification System (NZTCS) are currently classed as either ‘threatened’ or ‘at risk’ (Hitchmough *et al.* 2021), and a large proportion of New Zealand’s lizards now survive only on mammal-free offshore islands, or inside mammal-free fenced reserves on the mainland (Towns *et al.* 2001). When humans first arrived, New Zealand’s mammal fauna consisted of just three species of small insectivorous bats (King 1990), and while there is fossil evidence of other mammal species, including at least one mammal likely to have consumed small vertebrate prey, these species are likely to have been extinct for at least several million years (Hand *et al.* 2018; Worthy *et al.* 2006). Therefore, New Zealand lizards lacked experience with mammalian predators before several were introduced with two distinct waves of human colonization (Polynesians c. 1280 AD and Europeans c. 1800 AD). Introduced predators of lizards include cats, ferrets (*Mustela putorius furo*), stoats (*Mustela erminea*), weasels (*Mustela nivalis*), rats (*Rattus* sp.), mice (*Mus musculus*) and hedgehogs (*Erinaceus europaeus*) (Blackwell 2005; King 1990).

We aimed to establish whether New Zealand native lizards can recognize and respond to novel predator cues, and to assess the time scales over which antipredator responses can change. We measured the behaviour of two populations of McCann’s skink (*Oligosoma maccanni*) in response to different predation risk scenarios (treatments). Skink populations were sourced from an area of high mammalian predator density, and from within a conservation fence where mammalian predators have been absent

for 3–4 skink generations (Cree and Hare 2016). Treatments included the presentation of whole-body cues from an introduced predator (a live feral cat), visual cues of a coevolved predator (a model raptor) and an introduced predator’s olfactory cue (cat scent). Both skink populations coexist with native and introduced avian predators. McCann’s skink is a relatively common and widespread species listed as ‘non-threatened’ under the NZTCS (Hitchmough *et al.* 2021), which has persisted in areas with large and diverse predator populations. They are nonetheless found in nearly 60% of feral cat scats, with scats containing up to 45 individual lizards (Middlemiss 1995). It is therefore an ideal species to test whether any of New Zealand’s lizards have moved beyond Level 1 naiveté to mammalian predators.

We used this system to answer the following questions:

- a Can McCann’s skinks discriminate cues of an introduced mammalian predator, the feral cat, from procedural control cues?
- b Has the removal of introduced mammalian predators from a fenced reserve diminished the response of McCann’s skinks to predation risk?
- c Do McCann’s skinks balance the fitness benefits of predator avoidance against associated costs?

To answer these questions, we examined skinks’ basking behaviour because basking exposes them to greater predation risk. Because maximizing basking opportunities has direct links to increased fitness (Downes 2001), we predict that skinks will be able to discriminate and interpret predator cues to minimize risk by basking less frequently and/or in safer sites (i.e. closer to refuge). We also predict that while both populations would demonstrate a similar antipredator response to a raptor cue (a coevolved and ubiquitous threat), the population currently without mammalian predators would have a weaker antipredator response to cat cues than the skinks from the high-predator population, and that basking would be concentrated during the safest periods of each treatment day.

METHODS

Study sites and lizards

Skinks were collected from two populations near Macraes Flat in eastern Otago, New Zealand. Skinks from the ‘low-predator population’ were sourced from a fenced reserve (45°27′02″S, 170°26′20″E, 575 m a.s.l.) which has been free of all mammalian predators (excluding occasional incursions of house mice) since August 2006 (Reardon *et al.* 2012). Skinks from the ‘high-predator population’ came from ‘Golden Point’, a 20 ha reserve (11 km north of the fenced population; 45°20′58″S, 170°25′30″E, 340 m a.s.l.) with no formal predator control (DOC personal

communication, 2018) where skinks coexist with six potential predators—cats, ferrets, stoat, hedgehogs, Norway rats (*Rattus norvegicus*) and house mice—as confirmed by a camera survey conducted at the time of skink collection (99 trap nights). Introduced mammalian herbivores, including European rabbits (*Oryctolagus cuniculus*), red deer (*Cervus elaphus*) and feral pigs (omnivores; *Sus scrofa*), are also present in this area. Potential avian predators are ubiquitous across the region and include Australasian Harriers (*Circus approximans*; most frequently observed), New Zealand Falcons (*Falco novaeseelandiae*) and introduced Australian magpies (*Gymnorhina tibicen*), common starlings (*Sturnus vulgaris*) and little owls (*Anthene nocturna*) (Marchant *et al.* 2006; Reardon *et al.* 2012).

The vegetation of the region has been heavily modified by fire, land clearing and grazing and is a mosaic of introduced pasture grasses (e.g. *Agrostis capillaris*), native tussock (*Chionochloa rigida*, *C. rubra*) and shrublands dominated by native mānuka (*Leptospermum scoparium*) (Bibby 1997). While the high-predator site consisted of mostly tall, introduced grasses, and the low-predator site consisted of mostly native tussock grasses, the vegetation at the study sites had similar physical structure (Appendix S1).

We collected 32 adult skinks (16 males and 16 females) from each population in January 2018 using pitfall traps. Skinks were deemed adult if hemipenes were readily everted (males) or if individuals exceeded a minimum snout-vent length (SVL) of 49 mm (females) (Cree and Hare 2016). All skinks were likely to be at least two years old, based on the seasonality of births and the presence of smaller size classes. Captured skinks were transported to the laboratory for acclimation and behavioural testing and released at site of capture on completion of the study. The study took place after females had given birth, but during male spermiogenesis (Cree and Hare 2016) when basking is a key requirement (Saint Girons 1985). Given that reducing basking has high fitness costs, we predicted that male skinks would bask more frequently than female skinks.

Lizard husbandry

Each population was split into eight groups for housing, with four individuals of the same sex in each group (Female groups 1–4 and Male groups 1–4). All skinks were acclimated to the laboratory for a minimum of five days (Group 1 from each population) and a maximum of 26 days (Group 4 from each population) prior to commencing behavioural trials. Each group was housed in a 60-L clear plastic terrarium (W 45 cm × L 64 cm × H 34 cm), with a 5 cm deep sand/pebble substrate (builders pre-mix). Each terraria had a warm retreat/basking site (terracotta saucer, 11 cm diameter), situated 20 cm directly beneath a 42 W halogen lamp, a cool retreat site (9.7 cm × 15.2 cm wooden refuge with 1.2 cm gap height) and an area of vegetative cover (moss). Water was provided *ad libitum* and skinks were fed every 2–3 days on a combination of cut fruit (apricot/mango), pureed fruit mixed with protein powder and mealworms dusted in Calcium powder. Laboratory photoperiod was set to 12-h light (starting 08:00 h) and 12-h dark (starting 20:00 h). Basking lights in all housing terraria and the testing arenas were on for 7 h/day (09:00–16:00 h).

Experimental design and set-up

Behavioural trials were conducted over four consecutive weeks in January/February 2018 within 3.66 m diameter, 12-sided plastic-walled arenas with a 5 cm layer of sand/gravel substrate (Fig. 1c). Each arena had eight basking sites consisting of terracotta tiles (W 19.5 cm × L 19.5 cm × H 1.5 cm) positioned 15 cm beneath a 42 W (610 lumen) halogen lamp. Basking sites were arranged symmetrically in two parallel rows. On the ‘high-refuge’ side of the arena, refuges were added in close proximity (20–30 cm) to each basking site in one row. On the other ‘low-refuge’ side, the basking sites were more distant from refuge (1.2 m). Refuge consisted of tussocks (*Carex testacea*, similar in size and structure to tussocks at the field sites) and upturned terracotta saucers (13 cm diameter with a 2 × 2 cm access hole on the side, structurally similar to rock crevices at the field sites).

Skinks were acclimated in the testing arena for three days before the behavioural trials. A different group was tested each week. Groups from each source population were tested in one of two arenas, located in different rooms. The arena used for testing each population was alternated between weeks. Before testing, each skink was uniquely marked using a xylene-free paint pen. We also recorded (a) snout-vent length (SVL), (b) whether an individual had a tail-break (observable as an un-naturally short tail for skinks that had not regrown their tail to its pre-broken length, or as a change in patterning on the regrown tail), and (c) the vent to tail-break distance (a measure of tail-break severity). Skinks were then exposed to one of the four following treatments each day over successive days (Table 1): (a) procedural controls only, (b) cat scent, (c) a caged live female feral cat (Fig. 1a) and (d) a taxidermy harrier in flight (Fig. 1b). On each procedural control day, clean non-scented towelling (approximately 4 cm wide, washed twice at 55°C without detergent and air-dried) was placed over part of each basking tile the previous evening; an empty cage (L60 cm × W26 cm × H30 cm) was placed in the centre of each arena for 32 min each morning (starting 1 h after the basking lights came on) and 32 min each afternoon (starting 4 h after basking lights on); a pulley system running approximately 1.4 m above the arena substrate between the rows of high-refuge and low-refuge basking sites was moved by a hidden operator five times within a 26-min period, once in the morning (arena 1: starting 1 h 5 min after basking lights on; arena 2: starting 1 h 35 min after basking lights on) and again in the afternoon (arena 1: starting 5 h 5 min after basking lights on; arena 2: starting 4 h 35 min after basking lights on).

On treatment days, each of the above procedures was also followed, but with the following alterations. (1) Cat scent treatment: four basking sites in each arena (two ‘high-refuge’ sites at one end of the arena and two ‘low-refuge’ sites at the opposing end) were associated with towelling impregnated with cat body scent (towelling was placed in with bedding of two feral cats for one week, and frozen in a glass container for up to 10 days at –18°C before use), all other basking sites were associated with non-scented towelling identical to those used in the control procedure. (2) Cat treatment: the cage placed in the centre of the arena housed one of two black female feral cats, the individual

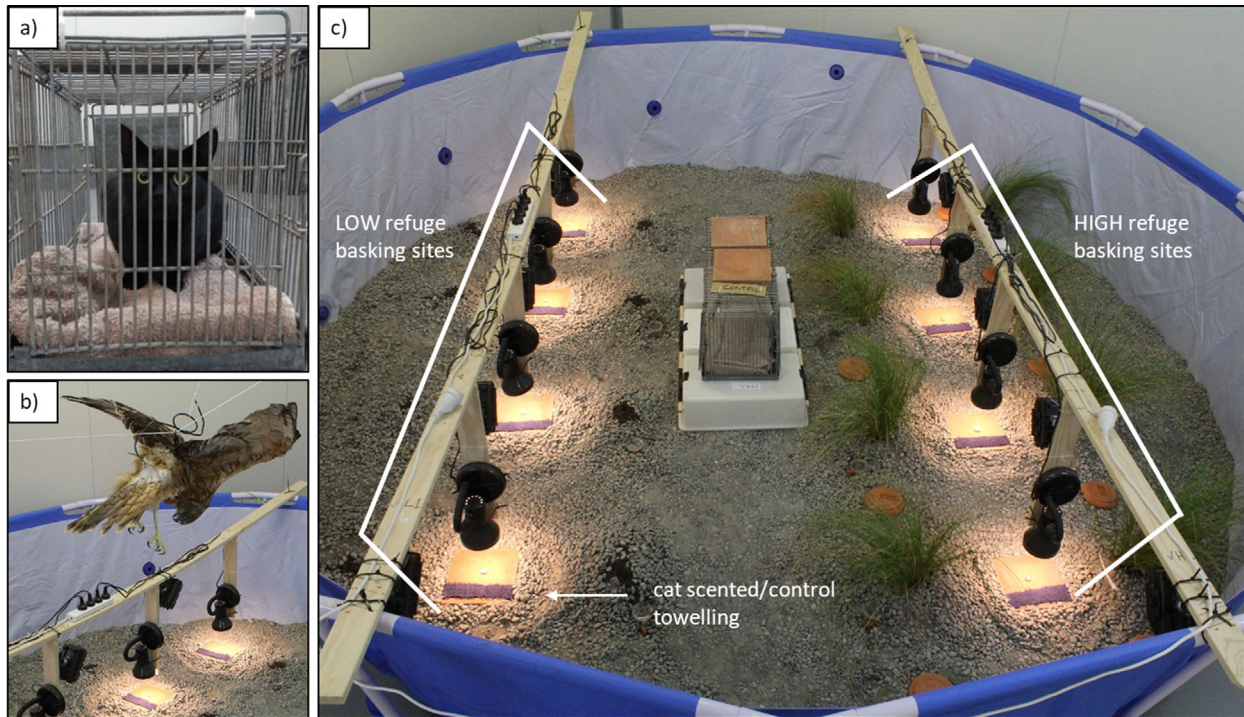


Fig. 1. Experimental set-up: a) a caged cat for the live cat exposure treatment; b) the taxidermy raptor attached to the pulley system; c) rows of four ‘low-refuge’ and four ‘high-refuge’ basking sites. Each basking site was associated with towelling for the cat scent trials and, when in use, the cage was placed in the centre of the arena.

Table 1. Predator exposures on each of the four treatment days (each day is represented by a separate column). Treatment exposures that differ to the procedural control are indicated in **bold**

Daily exposures	Ctrl	Cat scent	Cat	Raptor
Tile towelling (422 min)	no scent	½ with cat scent	no scent	no scent
AM Exposure 1 (32 min)	cage	cage	cage + cat	cage
AM Exposure 2 (26 min)	pulley	pulley	pulley	pulley + raptor
PM Exposure 1 (26 min)	pulley	pulley	pulley	pulley + raptor
PM Exposure 2 (32 min)	cage	cage	cage + cat	cage

cats were used in alternate arenas between the morning and afternoon exposure sessions. (3) Raptor treatment: a taxidermy Australasian Harrier mounted in an attacking position was attached to the pulley system and ‘flown’ across the arena.

Each basking tile had a camera (Bushnell HD Aggressor) positioned overhead, programmed to capture time-stamped images of the tile once every minute from 09:00 to 16:00 h. ‘Thermachron’ ibutton loggers were placed in the centre of each tile directly below the heat source, and one near each arena wall, and programmed to record the temperature once every hour for 24 h for the duration of the experiment. Ninety-five per cent of the 09:30–15:30 basking site readings fell between 24°C and 33°C, while the minimum ambient temperature recorded was 19°C. These temperatures are within the natural range experienced by this species at the field site, where the skinks are active between 16°C and 33°C (Holmes and Cree 2006).

Image processing and data analysis

The identity of all basking skinks, based on their painted markings (Appendix S2), was recorded via image tagging in ExifPro v2.1 (<http://www.exifpro.com>). An individual was considered to be basking when any part of its body crossed the basking tile in a photo, and not basking if no part of its body was on the basking tile. Images were excluded from analysis if less than half of the skink was visible because the skink was between the tile and the towel (970 or 2.87% of images excluded) or if it could not be identified definitively (e.g. skinks lying across each other; 280 or 0.83% images). We assumed that the number of images of a given skink on a basking tile equated to the number of minutes it was basking out of the fixed time period for which images were recorded (i.e. one image per minute per tile).

The response variable was modelled as a binomial distribution (Bernoulli trials >1), using the number of successes

(basking) and the number of failures (not basking). We used generalized linear mixed models and multimodel inference on these binomial data to model the effect of population (low or high predator), treatment (control, cat, cat scent or raptor), sex (male or female) and tile temperature (continuous between 27°C and 33°C) on the proportion of time that an individual spent basking under a given set of conditions. Firstly, we modelled the proportion of time spent basking vs. not basking. Secondly, we examined the preference for high-refuge tiles ('basking site preference') by modelling the proportion of time spent basking on high vs. low-refuge tiles and then repeated this analysis on basking sites with or without cat scent on treatment days when cat scent was used.

To test whether exposure to predators had a long-lasting temporal and spatial effect on avoidance, or whether avoidance was temporally targeted to periods of peak threat, we modelled the response separately for three time periods: (a) all day = 422 min/day; (b) during the 62 min/day cat exposure period (32 min in the morning, starting 60 min after the basking lights came on and 32 min in the afternoon, starting 240 min after basking lights on); and (c) during the 52 min/day raptor exposure period (26 min in the morning, starting 65–95 min after basking lights on and 26 min in the afternoon, starting 275–305 min after basking lights on) (there were no differences in behaviour between the morning and afternoon periods). For cat-scent treatment days, we compared basking sites treated with cat scent to those not treated with cat scent across all treatment days to separate preference for certain tiles from response to cat scent, which was present only on the cat-scent treatment day. Because previous studies have found links between behaviour and body size, or behaviour and tail-loss characteristics (Bateman and Fleming 2009), we tested for differences in SVL and tail-loss between populations (Welch's *t*-test) before modelling and used linear models to investigate whether these covariates affected basking.

For all analyses, we initially ran 15 candidate models (Appendix S3). All candidate models, including the null model, incorporated fixed effects for testing arena (two arenas), daily mean maximum temperature in each arena (continuous between 27°C and 33°C) and testing day for any given testing week (days 1–4). Random effects included the testing group (eight groups of eight skinks), individual skink ($N = 64$) and an observation-level random effect to account for data overdispersion ($N = 255$) (Harrison 2014). Candidate models other than the null model incorporated increasingly complex combinations of population ('P', levels: low predator, high predator), treatment ('Tr', levels: control, cat, cat scent and raptor) and sex ('S', levels: M, F) fixed effects, as well as interactions between these terms with the potential to be biologically meaningful if retained in the most highly ranked models using the AICc.

To analyse basking behaviour over the entire treatment day (*all day period*), or just the *cat exposure period* or the *raptor exposure period*, we used the same methods on subsets of the data. A number of models failed to converge for the cat and raptor exposure periods, which we solved by running simpler models that lacked an interaction term with temperature. This was justified by the lack of evidence for an effect of arena, temperature or testing day on basking site preference for the *all day period*. Some individuals were

rarely observed basking; therefore, when modelling basking site preferences for high vs. low-refuge sites, we removed observations for skinks when their total basking time was in the bottom quartile of observations or where they were observed basking on less than 50 images (*all day models*) or fewer than 10 images (*cat and raptor exposure period models*), in each instance selecting the higher cut-off.

Models were run using the *glmer* function from the *lme4* software package in R (Bates *et al.* 2014a; R Core Team 2017). Because all response variables were proportions, models used a binomial distribution with a logit link. All models used the 'bobqa' optimizer from the R package *minqa* (Bates *et al.* 2014b) with the maximum number of evaluations set to 100 000 to assist with model convergence. Given our sample size and the number of model parameters, we ranked all candidate models for each analysis using Δ AICc for small sample size (Burnham and Anderson 2002) and considered models to form part of a best model set if they had both a Δ AICc less than six and no simpler nested models with a lower Δ AICc (Richards 2008). We used the *MuMIn* package (Barton 2013) for model selection and to quantify marginal and conditional R^2 values (R^2_m and R^2_c , respectively), where R^2_m quantifies the variance explained by fixed effects alone, and R^2_c quantifies the variance explained by the entire model (incorporating both fixed and random effects) (Nakagawa *et al.* 2013). For any response variable where the fixed effects in the top-ranked model explained considerable variance (at least 18% of data variance—only the skink basking time models), we passed the top model (lowest AICc) to the *emmeans* package (Lenth 2018). This package calculated the marginal means (least-square means) for basking time with each predator cue treatment within each population. It also provided a graphical output of comparisons between treatments, odds ratios and adjusted *P*-values (Tukey multiplicity adjustment).

RESULTS

Skinks were recorded basking 19.4% of the time (32 518 out of 167 610 images) for a mean of 128 min/day (range 0–349 min). After removing records on days when basking was observed on less than 50 images, on average skinks basked at high-refuge sites 80% of the time ($n = 190$, range = 36–100%). The number of individuals that consistently basked above the 128 min/day average was skewed towards the low-predator population (15 of 19 individuals) and towards males (14 of 19 individuals).

Proportion of time spent basking

Source population, sex and predator cue treatments were all important predictors of the proportion of time that skinks spent basking and were included in the best-supported models for all testing periods (Appendix S4). Population and sex had a relatively large effect on basking that was consistent across all

treatments and all periods. Male skinks consistently basked more often than females (Fig. 2; mean difference 62 min/day), and skinks sourced from the low-predator population basked more than skinks from the high-predator population (Fig. 3; mean difference 68 min/day). In the best-supported model for each period (*all day*, *raptor exposure*, *cat exposure*), the fixed effects explained 18–37% of data variability.

Skinks altered their basking in response to predator cues and this response differed with source population (Fig. 3). A population \times treatment interaction was included in the most parsimonious models for both the *cat exposure period* and *raptor exposure period*, but not the *all day period* (Appendix S4). During the *cat exposure period*, skinks from the high-predator population reduced basking in the presence of a live cat (2.76 times less likely to bask) or cat scent with an empty cat cage (2.29 times less likely to bask), relative to the procedural control, but skinks from the low-predator population did not (Fig. 3, Table 2). Similarly, during the *raptor exposure period*, only skinks from the high-predator population reduced basking when exposed to a raptor cue (8.40 times less likely to bask) or to cat scent with the raptor pulley activated without the raptor (3.65 times less likely to bask) (Fig. 3, Table 2), relative to the procedural control.

Basking site preference

Source population, treatment, sex and temperature were all poor predictors of basking site preference, with any combination of these predictors explaining a maximum of 4% of the data variability (Appendix S5). Population was included in the best-supported model

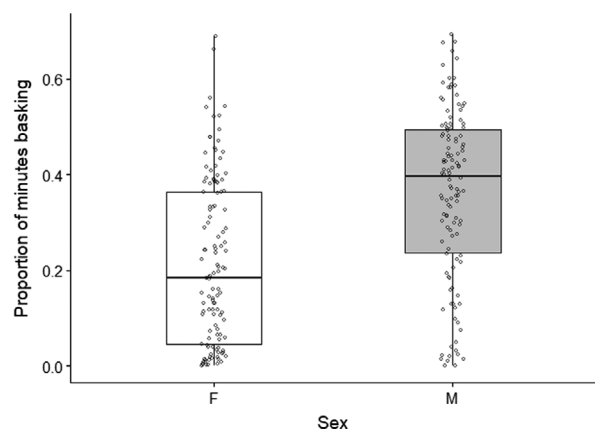


Fig. 2. Proportion of time basking by male (M) and female (F) skinks (includes data for all skinks for each treatment day, $n = 255$). Boxes show the median and interquartile range of the data; whiskers represent 1.5 times the interquartile range, or the range of the data, whichever is smaller.

for basking site preference over the *all day period* and for the *raptor exposure period*, although inference was weak given low explanatory power of these models. On average, all skinks preferred high-refuge over low-refuge basking sites, more so for skinks from the high-predator population during both exposure periods. The best-supported model for basking site preference during the *cat exposure period* included only a treatment effect. Both populations were more likely to bask at sites with high-refuge availability while a live cat was in the testing arena (cat treatment during *cat exposure period*) compared with the same period on days with only procedural controls. There was no evidence that skinks avoided cat-scented tiles. The null model was included in the candidate model set ($\Delta\text{AICc} = 0.50$), and at most 1% of data variability was explained by this variable. The effect size (0.38 ± 0.17) was also relatively small.

Temperature, skink size and tail breaks

The temperature of basking sites varied between arenas and across testing days (Appendix S6). Skinks from both populations increased basking at higher temperatures (Appendix S7). However, this relationship was much stronger among skinks from the high-predator population (linear regression; $F_{(126,127)} = 60.275$, $P < 0.001$, $R^2 = 0.32$) than from the low-predator population ($F_{(125, 126)} = 8.02$, $P = 0.005$, $R^2 = 0.06$). Skink size (SVL) did not vary between the high-predator (mean \pm SD = 59.7 mm \pm 3.5 mm) and low-predator (58.2 mm \pm 4.1 mm) populations ($t_{(60,82)} = 1.42$, $P = 0.16$). There was no relationship between SVL and proportion of time basking ($F_{(62,63)} = 2.94$, $P = 0.09$, $R^2 = 0.05$; Appendix S8), or SVL and preference for high or low-refuge basking sites (Linear regression; $F_{(53,54)} = 1.72$, $P = 0.19$). Tail breaks were discernible in 85% (54 of 64) of skinks and were equivalent between sexes (84% both sexes) and populations (88% and 81% in the low- and high-predator populations, respectively). However, tail-loss severity (measured as the vent to tail-break distance—the shorter this distance, the greater the severity) was significantly higher in the low-predator population (30.0 mm \pm 17.1 mm) compared with the high-predator population (56.0 mm \pm 17.7 mm) ($t_{(51,91)} = 5.51$, $P < 0.001$). Individuals with more extreme tail loss basked more frequently ($F_{(52,53)} = 4.69$, $P = 0.04$, $R^2 = 0.08$; Appendix S9). However, as individuals with more extreme tail loss were also disproportionately associated with the low-predator population, it was not possible to isolate the effect of tail loss extent from the broader effect of population. There was no relationship between severity of tail-loss and basking site preference ($F_{(44,45)} = 0.94$, $P = 0.33$).

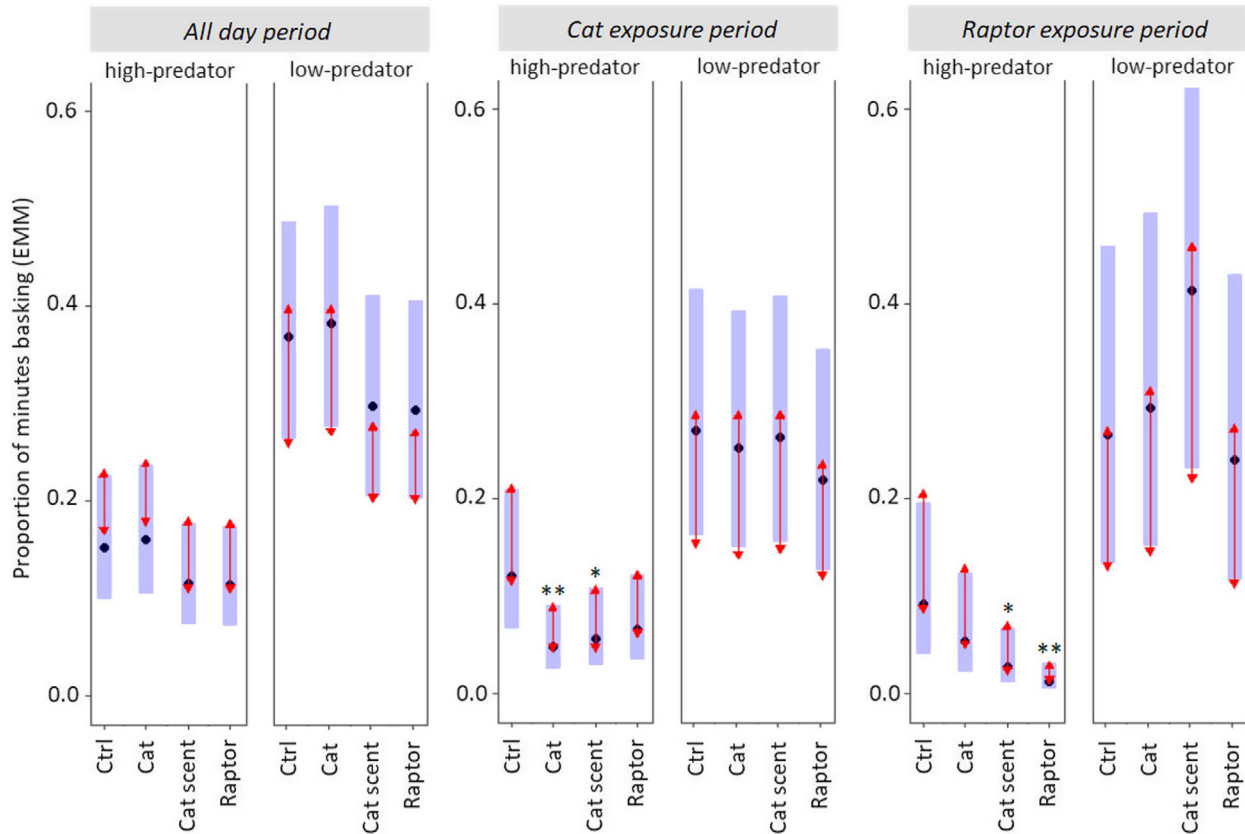


Fig. 3. Proportion of time basking by skinks during three periods: *all day period* (422 min/day), *cat exposure period* (62 min/day) and *raptor exposure period* (52 min/day). Points represent the estimated marginal means (EMM) and 95% confidence intervals (filled bars) for each population/treatment combination based on the best ranked model for each period (Appendix S4). Non-overlapping arrows indicate significant differences between groups within each model (adjusted $P < 0.05$, Tukey's HSD test). Within each population, responses to predator treatments that differ significantly from the control are indicated with asterisk ($*P < 0.05$, $**P < 0.001$).

DISCUSSION

Can McCann's skinks discriminate cues of feral cats from control cues?

Exposing skinks from the high-predator population to a live cat, and to cat scent alone, resulted in temporary reductions in basking. This suggests that for at least one species of New Zealand lizard, the period of exposure to a novel predator has been sufficient for the development of cue discrimination and an adaptive behavioural response. Feral cats are unlikely to have become established in the study area before the establishment of rabbits, approximately 150 years ago (King 1990); therefore, these adaptations have developed within a maximum of 50 skink generations (Cree and Hare 2016). Rapid development of antipredator behaviours to novel predator cues has been reported across a range of taxa, both within New Zealand and globally. Very rapid response times

include that of Ibiza wall lizards (*Podarcis pityusensis*) to the chemical cues of a snake within a decade of their introduction (Ortega *et al.* 2016) and evolution of innate predator recognition of an introduced red swamp crayfish (*Procambarus clarkii*) by tadpoles (*Pelophylax perezii*) within 20 years (Nunes *et al.* 2014). Examples from Australasia include nest-defence by New Zealand robins (*Petroica australis*) when confronted with visual cues of a stoat (within c. 100 years of exposure; Maloney and McLean 1995) and responses of two Australian lizards (*Morethia boulengeri* and *Christinus marmoratus*) and an Australian bush rat (*Rattus fuscipes*) to cat and fox scent cues (within 150 years of exposure; Carthey and Banks 2016; Webster *et al.* 2018).

Two previous studies found little evidence that New Zealand lizards from mammal-invaded areas (including *O. polychroma*, *O. zealandicum* and *Woodworthia maculata*) responded to the chemical cues of either ship rat (*Rattus rattus*) or hedgehog urine or faeces (Dumont 2015; Monks *et al.* 2019). Similarly,

Table 2. Marginal mean contrasts between treatments for each population (high-predator population (HPP) and low-predator population (LPP) where relevant) based on the top-ranked model for each exposure period. Period is all day (422 min/day), during the 62 min/day live cat exposure period, and during the 52 min/day raptor exposure period to test for evidence of a long-lasting temporal and spatial avoidance of predator threats (all day avoidance), or whether avoidance was temporally targeted to periods of peak threat (avoidance limited to the cat and raptor exposure periods). **Bold** indicates treatments that are significantly different from the control. *P*-values are adjusted using the Tukey method for comparing a family of four estimates. Tests are performed on the log odds ratio scale

Period	Population	Contrast	Odds ratio	SE	<i>z</i> -ratio	<i>P</i> -value
All day	Both	ctrl/cat	0.94	0.13	−0.44	0.97
		ctrl/cat scent	1.38	0.20	2.26	0.11
		ctrl/raptor	1.40	0.21	2.22	0.12
Cat exposure	HPP	ctrl/cat	2.76	0.74	3.79	<0.001
		ctrl/cat scent	2.29	0.63	3.02	0.01
		ctrl/raptor	1.95	0.52	2.49	0.06
	LPP	ctrl/cat	1.10	0.27	0.38	0.98
		ctrl/cat scent	1.04	0.25	0.16	1.00
		ctrl/raptor	1.32	0.34	1.07	0.71
Raptor exposure	HPP	ctrl/cat	1.79	0.65	1.61	0.37
		ctrl/cat scent	3.65	1.41	3.36	<0.01
		ctrl/raptor	8.40	3.34	5.34	<0.001
	LPP	ctrl/cat	0.08	0.29	−0.42	0.98
		ctrl/cat scent	0.51	0.16	−2.08	0.16
		ctrl/raptor	1.15	0.41	0.39	0.98

while a skink (*Caledoniscincus austrocaledonicus*) from New Caledonia (a nearby island with similar evolutionary history) avoids the chemical cues of recently introduced ship rats and cats, a native gecko (*Bavayia septuiclavis*) does not (Gerard *et al.* 2014). These studies may have failed to detect antipredator responses because of the cue type presented (Carthey and Banks 2014). We found stronger evidence of an antipredator response when visual cues of predators—a live cat and a model raptor—were presented than when lizards were exposed to chemical cues alone (although a direct comparison is difficult due to differences in the duration of exposure to each cue type). This supports previous suggestions that New Zealand lizards may rely heavily on non-chemical cues (e.g. visual, auditory) to detect and respond to predators (Monks *et al.* 2019). Because visual cues provide greater certainty of imminent predation risk, prey often respond more strongly to visual cues of a predator than to chemical cues (Carthey and Banks 2014). The response of New Zealand prey to visual cues may be amplified if visual cues have been an important means of detecting predators historically (Carthey and Banks 2014).

We compared skink responses only to procedural controls (i.e. empty cage, unscented towel and activated pulley), not to a novel scent, organism or object. Therefore, we were unable to tell whether skinks were responding to the cat, cat scent or raptor specifically, or just to the presence of a novel stimulus. Nevertheless, skinks from the high-predator population appeared to be more vigilant, in general, and

thus may have been responding to any cue that indicated potential danger.

Has the recent removal of introduced mammalian predators from a fenced reserve diminished skink responses to predation risk?

While the high-predator population temporarily reduced basking in the presence of a live cat, cat scent or a model raptor, the low-predator population did not reduce basking in the presence of any of these potential threats. This suggests that removal of mammalian predators has led to the loss of cat and raptor recognition within 3–4 skink generations. While lack of replication in our study meant that predator effects could not be separated from location effects, the results concur with the well-documented loss of predator recognition and antipredator behaviour following release from predation pressure in reptiles (Brock *et al.* 2015; Li *et al.* 2014) and other taxa (birds—Beauchamp 2004; e.g. mammals—Blumstein 2002; fish—Kelley and Magurran 2003). It often occurs very rapidly (Jolly *et al.* 2018b; Lapiedra *et al.* 2018; Muralidhar *et al.* 2019) because in lower-risk environments, excessive predator avoidance can have strong fitness costs, so selection can work to limit the retention of these behaviours (Smith and Blumstein 2008).

The recent removal of mammalian predators appears to have diminished not only the response by skinks to the risk posed by cats, but also to avian

predators. This was an unexpected result, given that skinks from the low-predator population coevolved with avian predators and continue to live in an area accessible to avian predators. A similar result has been recorded in a fish population, where it was concluded that isolation from one predatory threat (other predatory fish) diminished the antipredator response of prey fish towards a secondary predatory threat (predatory birds), even though exposure to this secondary predator threat continued (Wund *et al.* 2015). Additionally, a study on Aegean wall lizards (*Podarcis erhardii*) highlighted the importance of high-predator diversity in determining the retention rates of particular antipredator traits (Brock *et al.* 2015). These results suggest that the retention of antipredator behaviours is complex and often difficult to anticipate.

Do McCann's skinks balance the fitness benefits of predator avoidance against associated costs?

Basking is tightly coupled with fitness in lizards (Downes 2001), particularly for viviparous species in colder climates (Wapstra *et al.* 2010). To maximize fitness, lizards must balance avoiding predation with performing behaviours that maintain metabolism, such as basking. This balance will change with predation risk. In the low-predator population, the high cost of reducing basking for this temperate, viviparous species may have favoured individuals that bask more frequently regardless of predator cues. As basking behaviour is closely associated with fitness, it should be particularly sensitive to changes in predation pressure. This means that reductions in basking may have been lost rapidly with predator reductions, while other antipredator behaviours may not have changed at the same rate (Blumstein 2002). Rapid loss and gain of predator avoidance behaviours indicates flexibility in the response of McCann's skinks to spatial and temporal variation in predation risk, resulting from balancing risks and costs. By temporarily adjusting costly antipredator behaviours, skinks can limit the sub-lethal impacts associated with being overly wary during less risky periods. First, the high-predator population reduced basking during periods of peak risk (*cat* and *raptor exposure periods*) but not over longer time periods (*all day period*). Second, male skinks consistently basked more frequently than female skinks, regardless of population or treatment, presumably to maximize spermiogenesis (Van Damme *et al.* 1987). We would predict that females would be less willing to trade off less basking time under heightened predation risk at a different time of year, because of the metabolic costs of pregnancy.

How quickly and effectively prey populations are able to respond to changes in predation pressure

depends on the mechanisms underpinning the gain and loss of antipredator behaviours and the efficacy of antipredator responses (Carthey and Blumstein 2018). Priorities for future research include distinguishing among mechanisms and testing whether management actions (e.g. increasing refuge availability) can improve response efficacy. Potential mechanisms that allow prey to cope with changes in predation pressure include the following: (i) *labelling*, whereby a prey species uses the generalized features of a known predatory threat and applies it to novel threats; (ii) *rapid evolution*, whereby selective predation alters the frequency of prey population genotypes; or (iii) *learning*, whereby individuals develop behavioural responses following encounters with predators within their lifetime. The relative importance of these mechanisms could be determined using appropriate control treatments to test for labelling, comparing cue discrimination of captive-bred offspring *vs.* their wild-caught parents to test for evidence of rapid evolution (e.g. Jolly *et al.* 2018b; Wund *et al.* 2015), and comparing the response of individuals to predator cues over multiple exposures to test for learning (e.g. Li *et al.* 2014; Maloney and McLean 1995; West *et al.* 2018).

Differences in predator recognition abilities between prey species may provide a mechanistic hypothesis for patterns of species persistence and vulnerability. By conducting similar studies on a wider range of species that have different susceptibilities to predation, we may be able to determine the extent to which cue recognition contributes to the resilience of prey species in invaded systems. Therefore, the range of native species tested for acquisition of antipredator responses to introduced predators, and the range of cues tested, need to increase. Relatively few species from land masses where introduced predators are a major conservation threat have been tested for gain of antipredator responses. In New Zealand, this research has primarily focussed on the antipredator response of birds, with a more limited focus on other taxa. While our study has shown that one common species of skink in New Zealand alters their basking behaviour in the presence of cues representing an introduced predator, it is important to understand whether this ability is widespread among New Zealand's herpetofauna, given the high proportion that is threatened. Species that remain widespread, such as McCann's skinks, may have greater capacity to develop antipredator recognition and behaviours towards new predators, while species that are more threatened and declining may be less able to do so. We would predict that threatened species would remain naïve.

McCann's skink may not be representative as it is relatively resilient to introduced predators in the New Zealand context. Their populations remain

widespread and abundant, they have been known to replace other native skinks in certain habitats, and they are listed in the non-threatened minority of New Zealand herpetofauna (Hitchmough *et al.* 2021). Antipredator responses to a wider range of introduced predator cues also need to be tested. Only a few studies have tested the response of reptiles to non-human visual cues of predation risk (but see Li *et al.* 2014; Stapley 2004), despite evidence that reptiles often use visual cues to assess and respond to their immediate environment (e.g. Ammanna *et al.* 2014). In the New Zealand context, it would be useful to build on these experiments by repeating trials with visual as well as olfactory cues of other introduced predators (e.g. rats, hedgehogs, mustelids) to determine the extent to which skinks can generalize risk avoidance behaviour across the introduced predator guild.

CONCLUSIONS

Feral cats pose a significant threat to native prey species globally (Medina *et al.* 2011). Therefore, populations of the relatively common lizard species we studied remain vulnerable to cats, despite our encouraging results that suggest some New Zealand lizard species can reduce their evolutionary naiveté towards mammalian predators. The rapid loss of discrimination of both novel and coevolved predators in skinks from a population not exposed to mammalian predators indicates that predator removal can increase prey naiveté and render prey populations vulnerable once again to future increases in predation pressure. This means that predator incursions could be particularly damaging for prey populations exposed to few predators, highlighting the ongoing need for vigilant quarantine practices and fence maintenance (Muralidhar *et al.* 2019). It also highlights the risk of sourcing populations from predator-free islands or fenced sanctuaries for reintroductions into areas with higher predation pressure, at least in the short-term (Blumstein 2002; Jolly *et al.* 2018a).

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AUTHOR CONTRIBUTIONS

Hannah Cliff: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Menna Jones:** Conceptualization (equal); formal analysis (supporting); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal). **Christopher Johnson:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal). **Roger Pech:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal). **Bart Biemans:** Data curation (equal); investigation (equal). **Leon Barmuta:** Formal analysis (supporting). **Grant Norbury:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal).

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and reversed selection in Alaskan threespine stickleback fish. *Anim. Behav.* **106**, 181–9.

SUPPORTING INFORMATION

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

Data S1 Appendix S1: The vegetation structure at the source site for (a) the ‘high-predator’ skink population — the ‘Golden Point’ Department of Conservation (DOC) reserve and (b) the ‘low-predator’ skink population — one of the DOC managed mammal-exclusion fences at Macraes Flat (photos: Hannah Cliff).

Appendix S2: Camera trap image of two basking skinks with clear identifying marks.

Appendix S3: The 15 candidate models used for model selection.

Appendix S4: Summary of the best supported models ($\Delta AIC_c < 6$) for skink basking.

Appendix S5: Summary of the model sets for proportion of time basking at (a) high-refuge vs. low-refuge sites and (b) cat scented vs. control scented sites.

Appendix S6: Daily maximum temperature of ambient air (red), and each high-refuge (green) and low-refuge (blue) basking site, within each testing arena during the study.

Appendix S7: Relationship between basking site temperature and basking times for the high-predator (red) and low-predator (blue) populations. Basking times are taken from all four treatment days (not just the control day).

Appendix S8: The non-significant relationship between proportion of time basking (mean across four treatment days) and snout-vent length (SVL). Plot includes the line of best fit ($y = -0.01x + 0.935$) and 95% CI ($R^2 = 0.045$).

Appendix S9: The non-significant relationship between proportion of time basking (mean across four treatment days) and tail-break severity.