



Has an invasive lizard lost its antipredator behaviours following 40 generations of isolation from snake predators?

Annalise C. Naimo¹ · Cameron Jones² · David G. Chapple¹ · Bob B. M. Wong¹

Received: 20 April 2021 / Revised: 28 July 2021 / Accepted: 30 July 2021

© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

The introduction of species outside their native range is an insidious form of human-induced environmental change, with mounting evidence that behaviour, either through plastic behavioural responses or adaptive changes, can play a vital role in mediating invasion success. In particular, when species invade non-native habitats, they often leave behind native predators. Altered predator assemblages may then result in changes to antipredator responses overtime. Here, we capitalise on the well-characterised invasion history of an Australian reptile, the delicate skink, *Lampropholis delicata*, to investigate differences in antipredator responses between an invasive island population (Lord Howe Island) and its original mainland source (Coffs Harbour) following 40 generations of isolation. Specifically, we examined the responses of invasive and native skinks to scent cues taken from huntsman spiders, *Heteropoda* sp., a predator present in both populations, and red-bellied black snakes, *Pseudechis porphyriacus*, a predator absent from the invasive range. We measured the time skinks took to emerge from a shelter site and subsequent basking and foraging behaviours in the absence and presence of each predator scent. We did not detect any differences in responses between native and invasive skinks, although predator scent affected foraging behaviour. In a separate experiment, lizards were faced with a simulated bird strike and had the choice of retreating under a snake-scented or unscented shelter. When faced with such a threat, we found that skinks did not avoid snake-scented shelters. We also measured the activity and exploratory behaviour of each skink prior to exposure to predator cues, finding that increased activity and exploration appears to be linked to reduced antipredator behaviour for invasive but not native skinks. Contrary to our initial predictions, our results suggest that the relaxation of pressure from native predators may not necessarily translate to changes in key antipredator responses in invasive species, even after 40 generations of isolation.

Significance statement

Human movement introduce species into novel areas, where they are confronted with a suite of ecological challenges that must be navigated, including changes to predator assemblages, in order to successfully establish and become invasive. Altered predator assemblages encountered by invasive species may, in turn, result in changes to, or loss of, antipredator responses over time. We studied such a scenario in the delicate skink, an Australian lizard that has been repeatedly introduced to new areas. We compared the antipredator behaviour of skinks from an invasive island population to skinks from their original mainland source. We found that despite 40 generations of isolation, invasive skinks do not differ from native skinks in their antipredator behaviour. However, we found that greater activity and exploration levels had become linked to reduced antipredator behaviour in invasive but not native skinks.

Keywords Adaptation · Antipredator behaviour · Behavioural plasticity · Invasion · Personality · Predator avoidance

Communicated by C. R. Gabor.

David G. Chapple and Bob B. M. Wong joint senior authors

This article is a contribution to the Topical Collection Using behavioral ecology to explore adaptive responses to anthropogenic change – Guest Editors: Jan Lindström, Constantino Macias Garcia, Caitlin Gabor

Extended author information available on the last page of the article

Introduction

Antipredator behaviours can confer significant fitness benefits but can also be costly to perform (Lima and Dill 1990; Zanette and Clinchy 2020). For many prey species, the time and effort individuals spend in predator detection and avoidance can often come at the expense of other traits, such as

foraging behaviour (Downes 2001; Stapley and Keogh 2004) and reproductive success (Hua et al. 2014; Dillon and Conway 2018; Dulude-de Broin et al. 2020). Not surprisingly, it is well established that prey species respond adaptively to the presence of predatory threats and often adjust their behaviours accordingly to mitigate the risk of being captured and eaten (Atkins et al. 2019; Gaynor et al. 2019; Jolly et al. 2021). For example, in many species, vigilance is typically heightened in situations of greater predation risk (Elgar 1989; Zanette and Clinchy 2020). Prey species may also exhibit different antipredator responses when confronted with different kinds of predators and/or prioritise avoidance of certain predators over others depending on the different levels of threat these predators pose (Downes and Adams 2001; Head et al. 2002; Stapley 2004). For instance, Stapley (2003) found that southern grass skinks, *Pseudemoia entrecasteauxii*, were able to discriminate and preferentially avoid species of snakes that posed the greatest predation risk.

Within a species' range, different populations often co-occur with different predator assemblages. In this regard, the history of coexistence between predator and prey can act as a powerful selective force shaping the nature and extent of antipredator responses observed. For example, in velvet geckoes, *Oedura lesueurii*, populations that co-occur with broad-headed snakes, *Hoplocephalus bungaroides*, and exhibit stronger antipredator responses to the presence of snake odour cues compared to gecko populations that do not co-occur with broad-headed snakes (Downes and Adams 2001). In common wall lizards, *Podarcis muralis*, loss of antipredatory responses to snake cues was documented after several hundred years of geographic isolation (Durand et al. 2012). Indeed, a framework has been established by Carthey and Blumstein (2018) to predict how ecological and evolutionary interaction with predators can impact prey naiveté. This framework predicts that—in some scenarios—where an animal has previously shared evolutionary history with a specific predator but is no longer in current contact, the ability to discriminate the cues of that predator can be lost. In support of this, a number of studies have shown that antipredator responses can be rapidly lost or modified in prey species following isolation from predators, as in macropods living on islands with few or no predators (Blumstein et al. 2004; see also 'island syndromes', sensu Adler and Levins 1994), New Zealand robins, *Petroica australis australis*, housed in predator-free sanctuaries (Muralidhar et al. 2019), and garden skinks, *Lampropholis guichenoti*, reared in the absence of snakes (Downes 2001).

Individual personality differences mediate ecological interactions, which can, in turn, affect antipredator behaviour. Researchers have shown that animals can differ consistently in specific behavioural traits, including antipredator behaviour. For example, in convict cichlids, *Amatitlania nigrofasciata*, Jones and Godin (2010) found a strong

association between individuals' exploratory tendencies and their reaction to a novel threat, with more exploratory fish being slower to respond to a predator model. Similarly, in the chaffinch, *Fringilla coelebs*, more voracious feeders also respond more effectively to a model predator, even though foraging behaviour reduces time spent vigilant (Cresswell et al. 2003). Indeed, exposure to predation can generate correlated personality traits, shown in three-spined sticklebacks, *Gasterosteus aculeatus* (Bell and Sih 2007). These findings underscore the importance of considering personality as a factor when studying antipredator responses.

Here, we investigated the impact of altered predator assemblage on the behaviour of the invasive delicate skink, *Lampropholis delicata*, and the role of personality in mediating such responses. The delicate skink is a reptile native to mainland eastern Australia but has been accidentally introduced via movement of cargo to several Pacific islands, where it has successfully established and become invasive (Chapple et al. 2013; Moule et al. 2015; Tingley et al. 2016; Miller et al. 2017). Within its native range, the delicate skink is preyed upon by a variety of predators, including lizard-eating snakes, birds, and invertebrates (Cogger 2014). By contrast, snake predators are absent from some of the species' introduced range. The invasion history of the delicate skink, and the different predator assemblages encountered by source and invasive populations, provides an opportunity to investigate how recent release from certain predators (i.e. snakes) following the skink's introduction into novel island habitats might affect their behavioural responses when confronted with familiar versus unfamiliar predatory threats. Given that prey species are often confronted with a suite of different predatory threats in the wild, we were also interested in examining how such antipredator responses might be adjusted when skinks encounter multiple predatory threats simultaneously. Importantly, previous research has also found evidence of personality types in the delicate skinks being linked to different behavioural traits (Michelangeli et al. 2016, 2019), which provides a foundation for us to examine the effect of personality on antipredator responses, as well as potential insights into our understanding of the role of behaviour and behavioural variation in mediating the success of biological invasions.

On Lord Howe Island, lizards from the northern end of the island have a single source population from the Coffs Harbour region of northern New South Wales, Australia (Chapple et al. 2013; Moule et al. 2015), from which they arrived on the island in the late 1980s (Chapple et al. 2014). The delicate skink is likely to have arrived on Lord Howe Island as stowaways in a shipment of freight and cargo. In contrast to Coffs Harbour, snakes are absent on Lord Howe Island, but there are abundant avifauna and spiders that prey on delicate skinks in both the native and invaded populations (McCormick and Polis 1982; Marchant et al. 2006). Accordingly, we sought to test whether delicate skinks from the

invasive Lord Howe Island population respond to predators in the same way as skinks from the native Coffs Harbour source population.

We first looked at activity and exploratory behaviour in the absence of predators to quantify individual personality. Secondly, we examined the response of lizards to predatory chemical cues from the huntsman spider, *Heteropoda* sp., and red-bellied black snake, *Pseudechis porphyriacus*. The former is present in the ranges of both native and introduced populations and is known to prey on lizards (McCormick and Polis 1982). The red-bellied black snake, by contrast, is absent from Lord Howe Island but is abundant across the native range of the delicate skink, with skinks comprising up to one-third of the snake's diet (Cogger 2014). Thirdly, we simulated a scenario where lizards were subject to a strike from a model of a bird and were then given a choice between two shelter sites. One site was marked with snake scent cues, while the other was left unscented. The bird strike was simulated because birds are a key predator of the delicate skink across all ranges (Marchant et al. 2006) and the ability to respond to simultaneous predator threats has important implications for fitness (Head et al. 2002; Stapley 2004).

We expect that activity and exploration levels may differ between native and invasive skinks because of the role that activity and exploratory behaviour may play in aiding the establishment of a population in new areas (Chapple et al. 2012). Given the differences in predator assemblages between invasive and native ranges, when testing the behavioural responses of lizards to predator chemical cues, we predicted that both populations would respond to spider scent but that only the native range population would respond to snake scent. Snake-specific antipredator behaviours were expected to have been lost in Lord Howe Island skinks following ~40 generations without exposure to predatory snakes (e.g. Downes 2001; Blumstein et al. 2004; Muralidhar et al. 2019). In our multi-predator experiment, when confronted with the choice between retreat sites to avoid a simulated bird strike, lizards from the native population were expected to show a stronger preference for sheltering under the unscented shelter compared to the invasive population. Lastly, we hypothesised that personality would mediate anti-predatory responses of lizards, with more active and exploratory individuals showing bolder traits when exposed to predator cues and more likely to lose snake-specific responses on Lord Howe Island.

Materials and methods

Animal collection and husbandry

We collected adult male skinks by hand from the North Bay region of Lord Howe Island ($n=36$, $31^{\circ}30$ S, $159^{\circ}03$ E),

which our previous molecular work (Chapple et al. 2013; Moule et al. 2015) has shown to have a single native range source region (Coffs Harbour: $n=44$, $30^{\circ}21$ S, $153^{\circ}05$ E). A previous study has shown that hand capture of delicate skinks does not result in a biased sample of personality types (Michelangeli et al. 2016). Only males were used in this study because gravidity status can affect female behaviour, and it was not possible to determine the gravidity of field-collected females. Skinks from both populations were transported back to animal housing facilities at Monash University, Victoria, Australia, and individually marked with different colour combinations of visual implant elastomer (Northwest Marine Technology, Shaw Island, WA, USA; Michelangeli et al. 2019). The snout-vent length (SVL) of each individual was measured using digital callipers.

We housed skinks in groups of five to seven individuals in plastic containers (floor dimensions of 300×370 mm). This group size was chosen to emulate the high population densities the species is observed in the wild. Skinks were housed in temperature-controlled rooms ($22\text{--}23$ °C). At one end of each housing container, we provided a basking area using heat tape under a terracotta tile; this created a thermal gradient ($22\text{--}32$ °C) within the housing tub, allowing skinks to thermoregulate from 0800 to 1700 h, during which time UV lighting was activated above each housing container. Plastic pots and newspapers were added to provide shelter. The room was lit between 0700 and 2000 h daily. Skinks were given a constant water supply in a petri dish and fed a diet of crickets, *Acheta domestica*, dusted in a vitamin supplement (Reptivite) three times a week.

Experimental procedure

Skinks were housed in the laboratory for 4–6 weeks before the commencement of behavioural trials. To standardise for hunger levels, we fasted skinks for 24 h before each experiment. All trials were conducted in temperature-controlled rooms at 22 °C and recorded using JVC Everio GZ-E100 video cameras, then saved for later playback using BORIS (Friard and Gamba 2016). When these video recordings were scored, the researcher was blind to the treatment (i.e. origin and predator type). Equipment was thoroughly washed between trials with scentless non-toxic detergent to prevent scent contamination. An overview of our experimental protocol is provided in Fig. 1a.

Experiment 1: activity-exploration test

We used a protocol based on previously published studies (Goulet et al. 2017; Michelangeli et al. 2019, 2020) to measure activity and exploratory tendencies. Specifically, skinks were placed in an experimental arena (floor dimensions of 550×320 mm) marked with 20 equal grid squares. Skinks

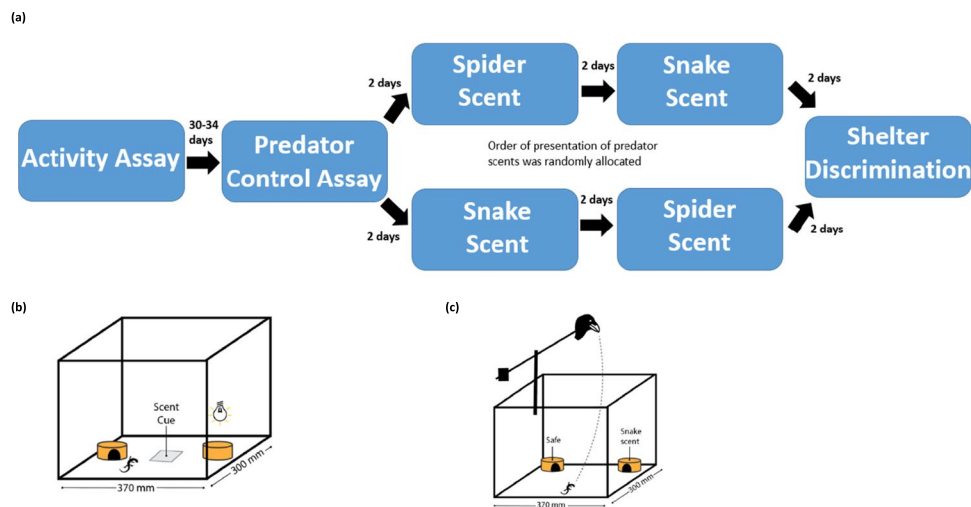


Fig. 1 **a** An overview of the experimental protocol and timing used in the study for delicate skinks (*Lampropholis delicata*) from Coffs Harbour and Lord Howe Island. **b** Arenas used for the snake-spider antipredator behaviour assays were fitted with a shelter site at one end and a basking site at the other. A cue (either unscented control, snake, or spider) was placed in the centre of the arena. After 10 min, a door

was removed from the shelter, and the skink was allowed to roam freely in the arena. **c** The arenas for the shelter discrimination assays were fitted with two shelters, with one at each end. One shelter was scented with a snake cue and the other with an unscented control. We simulated a predator attack by releasing a bird's head model to swoop towards the skink

were acclimated in the arena under a clear container for 10 min, and then, once the container was lifted, skinks were allowed to move freely throughout the arena for 20 min. We scored activity exploration as the number of transitions the skink made over the grid squares during this period. Previous studies have shown this measure to be repeatable and strongly correlated with exploratory behaviour among geographically distinct populations of the delicate skink (Goulet et al. 2017; Michelangeli et al. 2019, 2020). Therefore, this measurement was regarded as an accurate proxy for estimating both non-directed activity and exploratory behaviour, as outlined in Michelangeli et al. (2020).

Experiment 2: antipredator behaviour

Encounters with predators can elicit risk-averse behaviour. To measure how personality and invasion history can affect this response, we designed an experiment to test native and invasive lizards' response to huntsman spiders, predators they had previously encountered, and red-bellied black snakes, predators that the invasive population had not been exposed to for approximately 40 generations.

Predator scent collection

We collected scent cues from two different predator species of the delicate skink: the red-bellied black snake and the huntsman spider. We took scent from three individual snakes, housed by a private keeper and maintained on a diet of day-old chickens. We collected snake scent by

placing grade 1 qualitative filter paper in each snake's shelter for 14 days until the evening before each snake cue experiment. This method allows for the scent to transfer via physical contact onto an absorbent surface. We presented scents from all three snakes together in each snake scent trial to control for between-individual differences in scent or contact. We purchased five adult huntsman from Minibeast Wildlife (Kuranda, Queensland). The huntsman were individually housed in clear plastic containers throughout these experiments and fed crickets twice a week. We collected huntsman scent by placing grade 1 qualitative filter paper in each spider's container for 14 days, removing it the night before each experiment. We combined scents from all five spiders for each spider cue presentation. Skinks in the subfamily Eugongylinae, including *Lampropholis*, are able to discern between predator scent cues (i.e. spiders, snakes) and controls, with previous research showing that predator cues (delivered via bedding, as in our study) are sufficient to elicit drastic changes in a range of behavioural and life history traits across a myriad of contexts, from basking and foraging to sociality and predator avoidance (Downes and Shine 1999, 2001; Downes 2001, 2002; Downes and Hofer 2004; Head et al. 2002; Monks et al. 2019).

Antipredator assay

This assay was designed to measure antipredator behaviour in skinks when faced with a predator cue and valuable resources (a basking site and food object). The experimental

setup was adapted from previous similar studies (Downes 2001; Stapley 2004). We constructed experimental arenas (floor dimensions of 300×370 mm) with a shelter site at one end and a basking site at the other (Fig. 1b). In the middle of each arena, we placed either spider scent, snake scent, or an unscented piece of grade 1 qualitative filter paper as a control. The arena's layout meant that a skink would need to encounter the scent cue to pass from shelter to the basking site. Skinks were placed in shelters immediately before each assay. Each shelter was fitted with a door made from modelling clay, which prevented the skink from leaving the shelter and exploring the arena. After 10 min of acclimation within the shelter, an experimenter removed the door. Skinks were then allowed to move freely around the arena for 40 min, during which time we recorded latency to emerge from shelter and basking behaviour. To ensure that basking was measured independently of time spent sheltering, basking was calculated as the proportion of time each skink spent basking while out of the shelter for each trial. At the 40-min mark, a single cricket was placed into the centre of the arena, and we recorded foraging speed as the time taken for each skink to catch the cricket. This assay was repeated three times for each skink, once for every condition (control, spider, and snake). We presented unscented control first to gain a baseline measure of behaviour. We then presented the two different predator scents (i.e. snake or spider) in a random order in either the second or third trial.

Experiment 3: simultaneous predator threats

We carried out a separate experiment to investigate how isolation from snake predators on Lord Howe Island may influence how native range and introduced skinks respond to snake cues when simultaneously confronted with a threat by an avian predator (Stapley 2003). We used test arenas with two shelter sites at opposite ends (floor area of 300×370 mm, Fig. 1c). One shelter site was scented with a snake cue, as per experiment 2, and the other with an unscented control (sides were randomised to prevent a direction bias from influencing results). We rigged a large model of a bird to descend quickly into the arena, imitating a swoop attack. We placed skinks into a clear plastic acclimation chamber in the centre of the arena for 10 min. After 10 min, we removed the acclimation chamber and immediately released the bird model, which stopped approximately 5 cm above the skink's body. After this scare, we recorded each skink's time to enter a shelter and whether the safe or predator-scented shelter was chosen.

After the completion of experiments, all skinks were retained for future (unrelated) research.

Statistical analyses

All data were analysed using R (RStudio Version 1.1.463), with significance set to $\alpha=0.05$. We first constructed a linear model to test for population differences in activity-exploration scores, and these scores were used as our personality variable in later analyses.

To investigate the effect of personality and population on antipredator behaviour, we used linear mixed-effects models to analyse basking behaviour, and then Cox proportional hazards tests for both latency to emerge from shelter and foraging speed due to the right-censored nature of these data (Therneau et al. 2003). Mixed-effects models were constructed using the lme4 package (Bates et al. 2015) with Gaussian error distributions and survival analyses with multilevel Cox proportional hazards mixed effect models (package *coxme*, Therneau et al. 2003). All models contained fixed effects of population, treatment, activity-exploration score, SVL, and treatment presentation order. Interactions between population, treatment, and activity-exploration score were also included. Individual skink ID was included as a random effect to account for the repeated measures design. Models with and without interaction terms were compared using likelihood ratio tests. The best models for each response were retained based on Akaike information criteria (AIC) values. There was a significant interaction between population and activity-exploration score for latency to emerge and basking behaviour, so data were subset and models repeated for each population. As such, all discussion of population differences in latency to emerge and basking behaviour is based upon a comparison of separate models and is not statistically computed.

To analyse the effect of personality and population on the ability to balance simultaneous predator threats, we used survival analysis to measure latency to enter the shelter and a binomial generalised linear model to measure whether the safe or predator-scented shelter was chosen. Survival analyses were performed using Cox proportional hazards models. We included the fixed effects of population and activity-exploration score for both models and tested for an interaction between them.

Results

Experiment 1: activity-exploration test

We found that skinks from the invasive population had a significantly lower activity-exploration score than the native Coffs Harbour source population ($t = -3.68$, $df = 1$, $p < 0.001$).

Experiment 2: antipredator behaviour

Latency to emerge

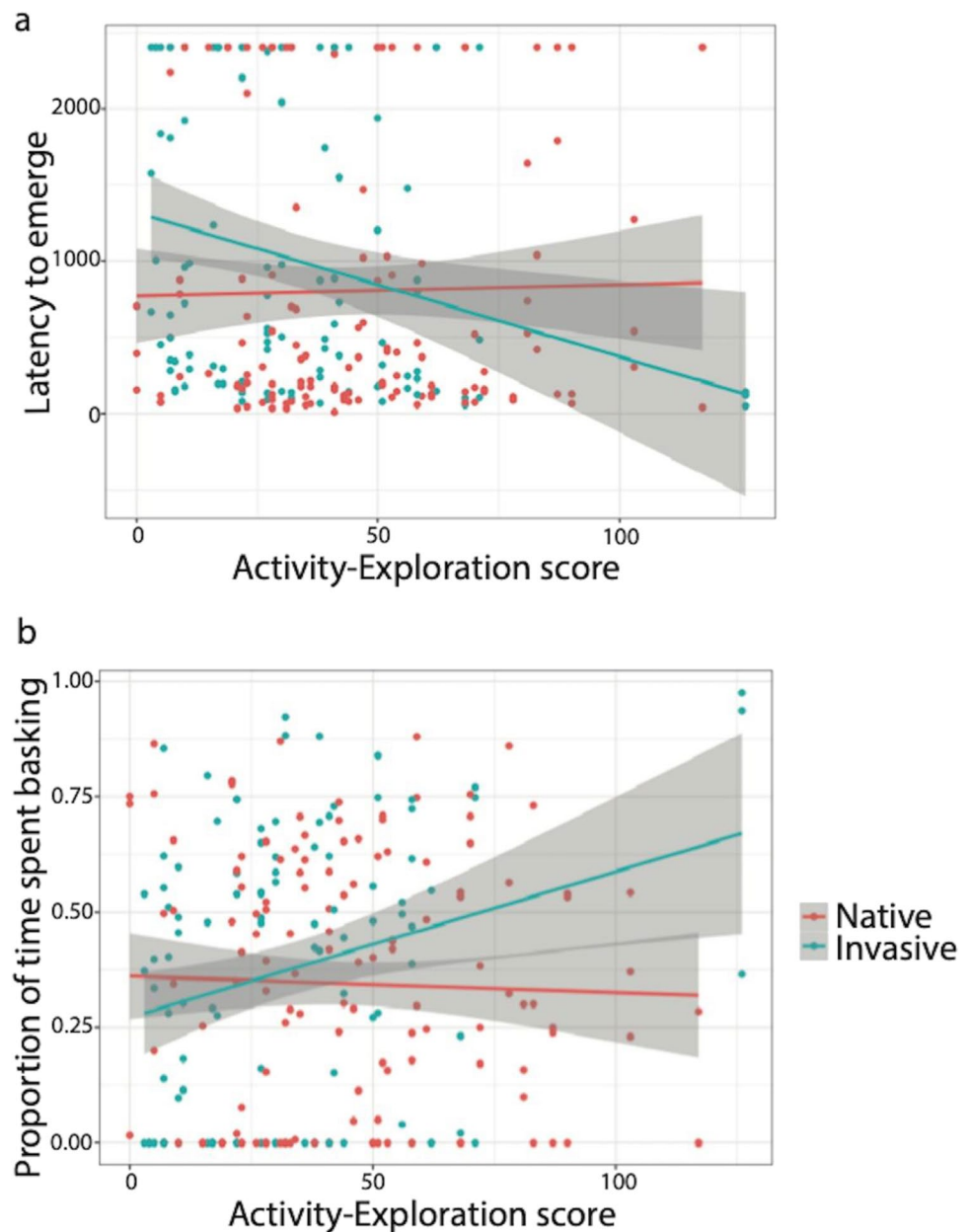
We found a significant interaction between activity-exploration score and population ($df=2$, $p=0.006$, Fig. 2a). As such, we analysed latency to emerge for each population separately. Lizards from Coffs Harbour exhibited no significant changes in latency to emerge in response either predator cues (snake $z=0.16$, $df=2$, $p=0.870$, spider $z=1.57$, $df=2$, $p=0.120$) or activity-exploration score ($z=0.16$, $df=1$, $p=0.345$). However, skinks from the invasive population with higher activity-exploration scores emerged sooner ($z=1.28$, $df=1$, $p=0.003$). Skinks from the invasive

population also showed an effect of presentation order, and took longer to emerge from shelter if first presented with a snake cue as opposed to a spider cue (estimate = -0.77 , $z = -2.32$, $df=1$, $p=0.020$).

Basking

We found evidence of a significant interaction between activity-exploration score and population ($df=2$, $p=0.009$, Fig. 2b), suggesting population-level differences in the association between personality types and basking. To disentangle this interaction, we explored each population separately. Lizards from Coffs Harbour did not differ in their basking behaviour when presented with snake or spider cues (snake

Fig. 2 The interaction between population and activity-exploration score in the delicate skink (*Lampropholis delicata*) for (a) latency to emerge and (b) basking behaviour. Grey areas around the trendlines denote a 95% confidence interval



$t = -0.10$, spider $t = 0.82$, $df = 2$, $p = 0.605$) and there was no effect of activity-exploration score on basking behaviour ($t = 0.01$, $df = 1$, $p = 0.988$). However, in the invasive population, basking was significantly associated with the activity-exploration score: more active-exploratory skinks also spent a greater proportion of time basking in the arena ($t = 2.89$, $df = 1$, $p = 0.004$). We found no effect of predator cues on basking behaviour in Lord Howe Island skinks (snake $t = 1.05$, spider $t = 0.36$, $df = 2$, $p = 0.567$).

Foraging speed

There was no interaction effect between population and activity-exploration score ($z = 0.50$, $df = 1$, $p = 0.391$). We found no evidence of population differences ($z = -1.05$, $df = 1$, $p = 0.863$), or effects of activity-exploratory score ($z = 0.79$, $df = 1$, $p = 0.104$) on foraging speed. Rather, skinks caught food items faster under both of the predator cue treatments, spider and snake scent, compared to control conditions (snake $z = 0.53$, spider $z = 0.43$, $df = 2$, $p = 0.023$).

Experiment 3: simultaneous predator threats

Latency to take shelter

When presented with multiple simultaneous predator threats, we found no difference between native and invasive skinks in their latency to take shelter ($z = -0.85$, $df = 1$, $p = 0.138$). We also found no effect of activity-exploration score ($z = 0.87$, $df = 1$, $p = 0.203$), or an interaction between population and activity-exploration score ($z = 0.01$, $df = 1$, $p = 0.995$).

Choosing a safe shelter

Overall, skinks chose the snake-scented shelter in 46.25% of trials, and the unscented shelter in 36.25% of trials, leaving 17.5% of trials where neither shelter was entered. We found no evidence of an interaction between population and activity-exploration score in choosing a safe shelter ($z = 0.59$, $df = 1$, $p = 0.552$). Neither population ($z = -0.83$, $df = 1$, $p = 0.546$) nor activity-exploration score ($z = -0.24$, $df = 1$, $p = 0.855$) had a significant effect on whether a skink chose the safe shelter over the one containing the predator scent.

Discussion

We found limited evidence for differences in antipredator behaviour between invasive skinks from Lord Howe Island, that have lived without snake predators for 40 generations, and skinks from their native Australian source population, where there is ongoing predation from snakes. Specifically,

in our study, we found that native skinks from Coffs Harbour and invasive skinks from Lord Howe Island do not alter their basking behaviour in response to either snake or spider cues. However, invasive skinks were more likely to modify their antipredator behaviour in response to the order of predator cues presented; they emerged slower from the shelter if first presented with a snake cue rather than a spider cue, suggesting invasive skinks may be more context-sensitive in their antipredator responses. We also did not find any differences in foraging latency between the native and introduced skinks. However, both populations foraged at a faster rate in the presence of predatory cues. We found that invasive skinks were significantly less active and exploratory than native skinks, and the association between activity-exploration score and antipredator behaviour also differed between the two populations. Specifically, we found that invasive skinks with higher activity-exploration scores exhibited riskier behaviour through increased basking and shorter emergence times in the presence of a predator cue. In contrast, there was no such relationship between activity-exploration score and antipredator behaviour in the native population. Lastly, we found no difference in the response of native and invasive skinks when presented with predator threats simultaneously, with no difference in either the latency for skinks to take shelter following a simulated bird strike or the likelihood of entering a snake-scented shelter.

Does the delicate skink alter its antipredator behaviour in its invasive range?

Invasive skinks on Lord Howe Island were less active and exploratory compared to skinks from their native source population. We had predicted that invasive skinks would be more active and exploratory as this may help them disperse into new habitats (Chapple et al. 2012). In this regard, increased exploratory behaviour has previously been shown in cane toads, *Rhinella marina*, where toads descending from range front individuals were also found to be more exploratory and bold than toads from the range core (Gruber et al. 2017). Further, invasive wall lizards, *Podarcis spp.* are more exploratory than their noninvasive congeners (Damas-Moreira et al. 2019). It is possible that different selection pressures on Lord Howe Island, other than differences in predator regimes, may have resulted in decreased activity and exploration in this population. For instance, reduced interspecific competition may have reduced the need for high activity levels and exploratory behaviours that may otherwise provide a selective advantage for individuals to find food or microhabitats. It is also likely that island effects have reduced selection for high levels of activity and exploration in the introduced Lord Howe Island population. Activity and exploration are traits associated with both predator-avoidance and dispersal, which can be selected against in

island ecosystems due to reduced predation pressure and the challenges of dispersal from the Island (e.g. see Roff 1990; Wright et al. 2016). So, whilst invasions on mainland areas might select for activity and exploratory behaviour (Gruber et al. 2017; Damas-Moreira et al. 2019), it may be the opposite in the case of invasions to small, oceanic islands.

We found differences in the relationship between activity-exploration score and antipredator between the two populations. In the invasive population, skinks with higher activity-exploration scores spent more time basking and emerged from shelter sooner than their counterparts when presented with a predator cue. However, there was no relationship between activity-exploration score and any other trait for skinks taken from the native population. We expected to find differences in the association between personality and antipredator behaviour between the two populations (Dingemans et al. 2007; Dingemans and Wolf 2013; Lapiedra et al. 2017). Indeed, other studies have reported differences in both the presence, and direction, of relationships between activity, exploration, and boldness amongst native delicate skink populations (Michelangeli et al. 2019). Michelangeli et al. (2019) previously identified a positive correlation between activity, exploration, and boldness in delicate skinks from the Coffs Harbour region, which was also sampled in this study. However, we did not find any evidence of a link between these traits in our study. One potential source of this difference is that the cue used in Michelangeli et al. (2019) was a physically simulated predator attack using a rod, in contrast to the predator scent used here. The emergence of correlated traits, like those found in invasive Lord Howe Island skinks, has also been shown in other invasive species. In fish, invasive *Xiphophorus helleri-maculatus* hybrids have developed correlations between aggression and exploratory behaviours after invading (D'Amore et al. 2019). Such correlation of potentially advantageous traits may form the basis of an 'invasion syndrome', which has been suggested to aid invasive species' establishment in novel areas (Chapple et al. 2012). Further studies could identify whether the correlated traits identified in this study have become correlated genetically (Mueller et al. 2017) or purely as a context-dependent phenotype, such as has been observed in other systems (Dingemans and de Goede 2004; van Oers et al. 2005).

We found that invasive skinks in our study did not differ from native skinks in their response to either spider or snake scent. This was expected for the spider scent due to ongoing predation from spiders in both populations (McCormick and Polis 1982). However, the lack of difference in native and invasive lizard responses to the snake scent was unexpected, especially given the ~40 generations in which invasive skinks have been freed from snake predation (Carthey and Blumstein 2018). A possible explanation is that the response to snake cues has been retained by the invasive population (Lahti et al. 2009). This could arise if there is little cost

associated with retaining such responses and/or because not enough generations have elapsed for the responses to have been lost. Another possibility is that the novel snake scent may have triggered a general neophobic response in invasive skinks unrelated to the snake scent's status as a predatory cue (Mettker-Hofmann et al. 2002). It is also possible that invasive skinks may have exhibited a more generalised antipredator response due to continued predator encounters on Lord Howe Island, and this enabled them to respond in the same way to spider and snake predator scents (Blumstein 2006). The predator community on Lord Howe Island has not been characterised in detail (e.g. distribution and relative density across the island; Chapple et al. 2014); however, we observed multiple predation attempts from Lord Howe Island currawongs and woodhens, and there is a high density of spiders on the island (ACN, personal observation). Thus, this high predator density on Lord Howe Island may have influenced our results. Lastly, it is important to acknowledge that other predator cues in nature, besides scent, may also be important in mediating adaptive prey responses (e.g. auditory, visual, and tactile). Future studies may therefore wish to explore how such cues, both in isolation and in combination with scent, might influence the behaviour of native and invasive skinks.

Response of the delicate skink to simultaneous predatory threats

We found no differences in our study between native and introduced skinks in their ability to balance simultaneous predator threats. Specifically, we found that when threatened by the imminent danger of a striking bird, there was no significant difference in the time taken for native and introduced skinks to enter a shelter or whether skinks selected the snake scented shelter over the unscented control. Here, we may have expected that if native range populations had recognised the cues of predatory snakes, they might have shown a stronger bias for, and preferentially selected, the unscented control shelter over the snake-scented shelter compared to the snake naïve Lord Howe Island skinks. Loss of snake antipredator behaviour following a period of naivety has been demonstrated in other lizard species (Downes 2001; Durand et al. 2012). Instead, the lack of difference in response between native and introduced skinks would suggest that the threat of a striking bird may have been prioritised over any potential risk that may have otherwise been posed by entering a shelter site containing snake cues and that this was the case even if skinks had recognised the snake cue as a potential threat. In that regard, our findings are comparable to those reported in another species of lizard, the southern grass skink (Stapley 2004). In that study, lizards were presented with the choice of retreat sites treated with the odour cues of two sympatric snake predators and were found to preferentially avoid the odour cues of the predator that posed the greater threat. Taken together, such findings

suggest that, when confronted with conflicting avoidance responses, prey may be flexibly prioritising avoidance of the more dangerous and imminent threat posed by the striking bird, irrespective of whether or not they recognise an alternative predatory threat.

Conclusions

In summary, we found that despite 40 generations in an environment with a reduced suite of predators, invasive skinks on Lord Howe Island do not appear to differ from native source skinks in their response to snake or spider cues, nor in their response to multiple simultaneous predator threats. We are unable to rule out the possibility that differences in behaviour initially existed following the colonisation of Lord Howe Island, and that these differences have eroded over generations through changes in selection pressure. Indeed, in the introductions in Hawaii and New Zealand, there is evidence for temporal shifts in behaviour (ACN et al. unpublished data), which could provide a promising springboard for further research. In the present study, native and invasive populations exhibited similar foraging behaviour, highlighting the importance of intraspecific competition in mediating foraging speed. Both populations caught prey quicker in the presence of predator cues and responded in the same way when presented with multiple simultaneous predator threats. Additionally, we found the island-dwelling invasive population to be less active-exploratory than its source, and we found individual levels of activity and exploration to predict some antipredator behaviour in invasive skinks but not native counterparts. This study suggests that changes to predator assemblages following the human-mediated introduction of species outside their native range do not necessarily result in changes to antipredator behaviour.

Acknowledgements We thank two anonymous reviewers for their constructive comments on the earlier version of this manuscript.

Author contribution All authors contributed to the study conception and design. Animal collection, data collection, and analysis were performed by ACN and CJ. The first draft of the manuscript was written by ACN, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This study was conducted with funding support from the Australian Research Council (DP170100684, to DGC and BBM), National Science Foundation Graduate Research Opportunities Worldwide Program (to CJ), and Australian Government Research Training Program (to ACN).

Availability of data All data are available via FigShare (<https://doi.org/10.26180/14451129.v2>).

Code availability All code is available via FigShare (<https://doi.org/10.26180/14451129.v2>).

Declarations

Ethics approval and consent to participate This study was conducted with animal ethics approval from Monash University (approval number 16736), and New South Wales (LHIB 09/18) and Victorian (permit number 10008946) scientific research permits. All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Competing interests The authors declare no competing interests.


References

- Adler GH, Levins R (1994) The island syndrome in rodent populations. *Q Rev Biol* 69:473–490
- Atkins JL, Long RA, Pansu J, Daskin JH, Potter AB, Stalmans ME, Tarnita CE, Pringle RM (2019) Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* 364:173–177
- Bates D, Machler M, Bolker B, Walker S (2015) Fitting linear mixed-effect models using lme4. *J Stat Softw* 67:1–48
- Bell AM, Sih A (2007) Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecol Lett* 10:828–834
- Blumstein DT (2006) The multipredator hypothesis and the evolutionary persistence of antipredator behavior. *Ethology* 112:209–217
- Blumstein DT, Daniel JC, Springett BP (2004) A test of the multipredator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. *Ethology* 110:919–934
- Carthey AJ, Blumstein DT (2018) Predicting predator recognition in a changing world. *Trends Ecol Evol* 33:106–115
- Chapple DG, Simmonds SM, Wong BBM (2012) Can behavioral and personality traits influence the success of unintentional species introductions? *Trends Ecol Evol* 27:57–64
- Chapple DG, Miller KA, Kraus F, Thompson MB (2013) 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* 19:134–146
- Chapple DG, Miller KA, Chaplin K, Barnett L, Thompson MB, Bray RD (2014) Biology of the invasive delicate skink (*Lampropholis delicata*) on Lord Howe Island. *Aust J Zool* 62:498–506
- Cogger H (2014) Reptiles and amphibians of Australia. CSIRO Publishing Melbourne
- Cresswell W, Quinn JL, Whittingham MJ, Butler S (2003) Good foragers can also be good at detecting predators. *Proc R Soc Lond B* 270:1069–1076
- Damas-Moreira I, Riley JL, Harris DJ, Whiting MJ (2019) Can behaviour explain invasion success? A comparison between sympatric invasive and native lizards. *Anim Behav* 151:195–202
- D'Amore DM, Popescu VD, Morris MR (2019) The influence of the invasive process on behaviours in an intentionally introduced hybrid, *Xiphophorus helleri-maculatus*. *Anim Behav* 156:79–85
- Dillon KG, Conway CJ (2018) Nest predation risk explains variation in avian clutch size. *Behav Ecol* 29:301–311
- Dingemanse NJ, de Goede P (2004) The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behav Ecol* 15:1023–1030
- Dingemanse NJ, Wolf M (2013) Between-individual differences in behavioural plasticity within populations: causes and consequences. *Anim Behav* 85:1031–1039
- Dingemanse NJ, Wright J, Kazem AJ, Thomas DK, Hickling R, Dawnay N (2007) Behavioural syndromes differ predictably

- between 12 populations of three-spined stickleback. *J Anim Ecol* 76:1128–1138
- Downes S (2001) Trading heat and food for safety: costs of predator avoidance in a lizard. *Ecology* 82:2870–2881
- Downes SJ (2002) Does responsiveness to predator scents affect lizard survivorship? *Behav Ecol Sociobiol* 52:38–42
- Downes SJ, Adams M (2001) Geographic variation in antisnake tactics: the evolution of scent-mediated behavior in a lizard. *Evolution* 55:605–615
- Downes S, Hoefler AM (2004) Antipredatory behaviour in lizards: Interactions between group size and predation risk. *Anim Behav* 67(3):485–492
- Downes SJ, Shine R (1999) Do incubation-induced changes in a lizard's phenotype influence its vulnerability to predators? *Oecologia* 120:9–18
- Downes SJ, Shine R (2001) Why does tail loss increase a lizard's later vulnerability to snake predators? *Ecology* 82:1293–1303
- Dulude-de Broin F, Hamel S, Mastromonaco GF, Côté SD (2020) Predation risk and mountain goat reproduction: evidence for stress-induced breeding suppression in a wild ungulate. *Funct Ecol* 34:1003–1014
- Durand J, Legrand A, Tort M, Thiney A, Michniewicz RJ, Coulon A, Aubret F (2012) Effects of geographic isolation on anti-snakes responses in the wall lizard, *Podarcis muralis*. *Amphibia-Reptilia* 33:199–206
- Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev* 64:13–33
- Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol Evol* 7:1325–1330
- Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS (2019) Landscapes of fear: spatial patterns of risk perception and response. *Trends Ecol Evol* 34:355–368
- Goulet CT, Thompson MB, Michelangeli M, Wong BBM, Chapple DG (2017) Thermal physiology: a new dimension of the pace-of-life syndrome. *J Anim Ecol* 86:1269–1280
- Gruber J, Brown G, Whiting MJ, Shine R (2017) Geographic divergence in dispersal-related behaviour in cane toads from range-front versus range-core populations in Australia. *Behav Ecol Sociobiol* 71:38
- Head ML, Keogh JS, Doughty P (2002) Experimental evidence of an age-specific shift in chemical detection of predators in a lizard. *J Chem Ecol* 28:541–554
- Hua F, Sieving KE, Fletcher RJ Jr, Wright CA (2014) Increased perception of predation risk to adults and offspring alters avian reproductive strategy and performance. *Behav Ecol* 25:509–519
- Jolly CJ, Smart AS, Moreen J, Webb JK, Gillespie GR, Phillips BL (2021) Trophic cascade driven by behavioural fine-tuning as naïve prey rapidly adjust to a novel predator. *Ecology* 102:e03363
- Jones KA, Godin J-GJ (2010) Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. *Proc R Soc Lond B* 277:625–632
- Lahti DC, Johnson NA, Ajie BC, Otto SP, Hendry AP, Blumstein DT, Coss RG, Donohue K, Foster SA (2009) Relaxed selection in the wild. *Trends Ecol Evol* 24:487–496
- Lapiedra O, Chejanovski Z, Kolbe JJ (2017) Urbanization and biological invasion shape animal personalities. *Glob Change Biol* 23:592–603
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Marchant S, Higgins PJ, Ambrose SJ, Steele WK (2006) Handbook of Australian, New Zealand and Antarctic birds. Oxford University Press, Melbourne
- McCormick S, Polis GA (1982) Arthropods that prey on vertebrates. *Biol Rev* 57:29–58
- Mettke-Hofmann C, Winkler H, Leisler B (2002) The significance of ecological factors for exploration and neophobia in parrots. *Ethology* 108:249–272
- Michelangeli M, Wong BBM, Chapple DG (2016) It's a trap: sampling bias due to animal personality is not always inevitable. *Behav Ecol* 27:62–67
- Michelangeli M, Chapple DG, Goulet CT, Bertram MG, Wong BBM (2019) Behavioral syndromes vary among geographically distinct populations in a reptile. *Behav Ecol* 30:393–401
- Michelangeli M, Melki-Wegner B, Laskowski K, Wong BBM, Chapple DG (2020) Impacts of caudal autotomy on personality. *Anim Behav* 162:67–78
- Miller KA, Duran A, Melville J, Thompson MB, Chapple DG (2017) Sex-specific shifts in morphology and colour pattern polymorphism during range expansion of an invasive lizard. *J Biogeogr* 44:2778–2788
- Monks JM, Nelson NJ, Daugherty CH, Brunton DH, Shine R (2019) Does evolution in isolation from mammalian predators have behavioural and chemosensory consequences for New Zealand lizards? *NZ J Ecol* 43:3359
- Moule H, Chaplin K, Bray RD, Miller KA, Thompson MB, Chapple DG (2015) A matter of time: temporal variation in the introduction history and population genetic structuring of an invasive lizard. *Curr Zool* 61:456–464
- Mueller JC, Edelaar P, Baños-Villalba A, Carrete M, Potti J, Blas J, Tella JL, Kempnaers B (2017) Selection on a behaviour-related gene during the first stages of the biological invasion pathway. *Mol Ecol* 26:6110–6121
- Muralidhar A, Moore FL, Easton LJ, Jamieson IG, Seddon PJ, van Heezik Y (2019) Know your enemy? Conservation management causes loss of antipredator behaviour to novel predators in New Zealand robins. *Anim Behav* 149:135–142
- Roff DA (1990) The evolution of flightlessness in insects. *Ecol Monogr* 60:389–421
- Stapley J (2003) Differential avoidance of snake odours by a lizard: evidence for prioritized avoidance based on risk. *Ethology* 109:785–796
- Stapley J (2004) Do mountain log skinks (*Pseudemoia entrecasteauxii*) modify their behaviour in the presence of two predators? *Behav Ecol Sociobiol* 56:185–189
- Stapley J, Keogh JS (2004) Exploratory and antipredator behaviours differ between territorial and nonterritorial male lizards. *Anim Behav* 68:841–846
- Therneau T, Grambsch P, Pankratz VS (2003) Penalized survival models and frailty. *J Comput Graph Stat* 12:156–175
- Tingley R, Thompson M, Hartley S, Chapple DG (2016) Patterns of niche filling and expansion across the invaded ranges of an Australian lizard. *Ecography* 39:270–280
- van Oers K, Klunder M, Drent PJ (2005) Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behav Ecol* 16:716–723
- Wright NA, Steadman DW, Witt CC (2016) Predictable evolution toward flightlessness in volant island birds. *PNAS* 113:4765–4770
- Zanette LY, Clinchy M (2020) Ecology and neurobiology of fear in free-living wildlife. *Ann Rev Ecol Evol S* 51:297–318

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Authors and Affiliations

Annalise C. Naimo¹ · Cameron Jones² · David G. Chapple¹  · Bob B. M. Wong¹

✉ David G. Chapple
david.chapple@monash.edu

² Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

¹ School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia