

Reintroducing native predators improves antipredator responses in naïve prey

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Prey animals may lack appropriate predator avoidance behaviours to novel predators, which has contributed to the decline of many species worldwide following human introduction of novel predators. Excluding novel predators from conservation reserves has been used to attempt to recover naïve species with mixed success. However, in the absence of predators, prey naïveté can be exacerbated. Reintroducing native predators has been suggested as a solution to addressing this problem and may act as a stepping stone to improve behavioural responses to novel predators. We tested the behavioural responses of two prey species, the burrowing bettong, *Bettongia lesueur*, and spinifex hopping mouse, *Notomys alexis*, to the reintroduction of a native predator, the western quoll, *Dasyurus geoffroyi*, and determined whether exposure to a native predator improved their antipredator responses to introduced feral cats, *Felis catus*. Quoll-exposed bettongs spent less time engaged in inattentive foraging behaviours compared to control (nonpredator exposed) bettongs but did not discriminate between predator and nonpredator visual or olfactory cues (native or novel). Quoll-exposed spinifex hopping mice modified their foraging in open habitats and increased wariness in the presence of quoll stimuli, whereas cat-exposed hopping mice only exhibited increased wariness in the presence of cat stimuli. Our results show that reintroductions of native predators improved general antipredator responses in native prey species, but there was only weak evidence that this led to an improved response to introduced predators. However, reintroducing native predators improved general antipredator behaviour in ontogenetically naïve populations which may make them more suitable for releases outside conservation fences where novel predators are present.

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Animals that have been isolated from native predators or that evolved in isolation from novel predators often lack the appropriate behaviours to detect and avoid the latter (Banks et al., 2018; Berger et al., 2001; Carthey & Banks, 2014). As such, 'prey naïveté' has been documented as a major factor in the worldwide decline of species (Salo et al., 2007; Sih et al., 2010). In Oceania, prey naïveté towards introduced predators has contributed to the decline and extinction of native mammals and birds, and in response many extant threatened species have been moved to islands or fenced conservation reserves to protect them from introduced predators (Blackburn et al., 2004; Carthey & Blumstein, 2018; Legge et al., 2018).

While fenced conservation reserves are effective at conserving species in the short term (Legge et al., 2018; Moseby et al., 2011), they create other challenges for wildlife management as they can limit dispersal, increase the chances of inbreeding, cause overpopulation in the absence of predators and exacerbate the issue of prey naïveté (Blumstein & Daniel, 2005; Carthey & Banks, 2014; Harrison et al., 2023; Jolly et al., 2018; Moseby, Lollback, et al., 2018). Attempts to reintroduce some of these 'naïve' species to their original ranges (i.e. not within fenced conservation reserves) have failed due to predation by introduced predators (Bannister et al., 2016; Christensen & Burrows, 1995; Morris et al., 2021; Moseby et al., 2011). In attempting to improve predator responses in prey species, researchers have proposed exposing them to novel predators under wild conditions (Makin et al., 2018; Moseby et al., 2018a; 2018b). Initial results are encouraging (Blumstein et al., 2019; Moseby et al., 2022; Ross et al., 2019; Tay et al., 2021), but

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some species remain susceptible to introduced predators (Radford et al., 2018). For instance, exposing naïve prey to native predators may act as a stepping stone to overcoming evolutionary naiveté to introduced predators (Van der Weyde et al., 2023). While some changes in prey behaviour have been documented in response to reintroduction of dasyurids in Australia (Cunningham et al., 2019; Jolly et al., 2021; Waaleboer et al., 2024), relative to the number of predator reintroductions undertaken, changes in prey behaviour in response to the reintroduction of a native predator are largely unknown (Stepkovitch et al., 2022).

In this study, we first investigated whether the reintroduction of a native predator (western quoll, *Dasyurus geoffroyi*) has resulted in changes to antipredator behaviour in two prey species inside a fenced reserve: the burrowing bettong, *Bettongia lesueur*, and spinifex hopping mouse, *Notomys alexis*. Both hopping mice and bettong have been ontogenetically isolated from quolls for generations. Bettongs were reintroduced to the study site from island populations (therefore isolated from quolls for 7000 years; Lewis et al., 2013) and hopping mice have not been exposed to quolls for 200 years (since quolls became extinct in the region). We then tested whether exposure to native quolls also improved their ability to respond to stimuli of an introduced predator, the feral cat, *Felis catus*. Both prey species are known prey of both predators where they both occur (Bannister et al., 2021; Stepkovitch et al., 2023; West, Tilley, et al., 2019). Hopping mice are found throughout the study region so we were able to test the difference in their behaviour between quoll-exposed (inside the reserve), cat-exposed (outside the reserve) and control populations (inside with electrified fences which excludes both cats and quolls) simultaneously. Bettongs could only be compared between quoll-exposed and control as they are not present outside the reserve.

We predicted that quoll-exposed bettongs would be more wary, have greater flight initiation distances and greater vigilance while foraging compared with control bettongs (nonquoll-exposed populations). If bettongs perceive quolls and cats as similar ‘predator’ archetypes (Carthey & Blumstein, 2018; Cox & Lima, 2006; Glen & Dickman, 2005), then quoll-exposed bettongs will have similar behavioural responses to cat and quoll predator stimuli relative to control stimuli while control bettongs will respond similarly to all stimuli (quoll, cat, rabbit, control). Furthermore, their behaviour in the quoll-exposed treatment will be similar to that recorded in bettongs exposed to cats in a previous study (West et al., 2018). We predicted that predator-exposed spinifex hopping mice (quoll-exposed and cat-exposed) will (1) spend more time foraging and have lower giving-up densities (GUD; Bedoya-Perez et al., 2013) in low-predation-risk habitat (covered; Morris et al., 2015) and (2) respond appropriately to predator stimuli and not respond to controls because Australian rodents recognize predator archetypes (Cox & Lima, 2006), whereas control spinifex hopping mice will spend similar amounts of time foraging and have similar GUDs across all habitats and stimuli.

METHODS

Study Species

Burrowing bettongs are bipedal, medium-sized, nocturnal marsupials (1.5 kg) that live communally in burrow systems (Short & Turner, 1999). Owing to the spread of introduced predators following European settlement, the bettong became extinct on mainland Australia but has persisted on three offshore islands (Short & Turner, 2000). Spinifex hopping mice are small rodents that are widely distributed throughout the Australian arid zone, occupying sand dune and tussock grassland habitats (Breed, 1998; Watts & Aslin, 1981). Hopping mice live in social groups, and sleep

in burrow systems which are evident from circular popholes (vertical openings) on the surface and can have multiple entrances (Thompson & Thompson, 2007). Predation on hopping mice by feral cats and foxes, *Vulpes vulpes*, has been well documented in the arid zone (Paltridge et al., 1997; Read & Bowen, 2001; Spencer et al., 2014a). The average generation length for bettongs is estimated as 3 years, whereas for hopping mice it is estimated at just under 2 years (Pacifi et al., 2013).

Study Area

Arid Recovery is a 123 km² private conservation reserve in arid South Australia that is separated into six experimental exclosures (Fig. 1) surrounded by a 1.8 m high floppy top fence (Moseby et al., 2011). The fence is designed to exclude introduced cats, foxes and rabbits, *Oryctolagus cuniculus* (Moseby & Read, 2006). Rabbits, cats and foxes have been removed from four exclosures (Main, First, Second, Northern) totalling 60 km² and bettongs were reintroduced from island populations to this area in 1999. Hopping mice were locally rare in the region prior to the establishment of Arid Recovery, but were rerecorded in the region after 1997 and first recorded inside the reserve in 1999 (Moseby et al., 2009). Since the exclusion of feral predators, hopping mice abundance has increased up to 15 times compared with their abundance outside the reserve (Moseby et al., 2009). Inside the reserve, both bettongs and hopping mice are still exposed to predation from reptiles and nocturnal raptors. Quolls were reintroduced to the First, Second and Northern sections of the reserve as a trial in 2014 and 2015 and as a full release in 2018. They currently coexist with bettongs and hopping mice.

In this study, our control treatment was the feral-free exclosure (Main Exclosure, 1400 ha) where bettongs and hopping mice were

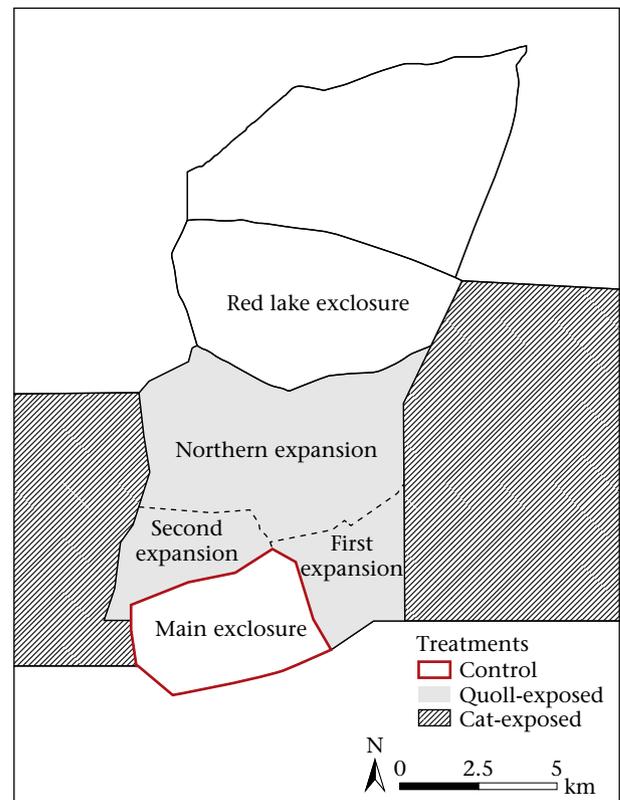


Figure 1. Map of the Arid Recovery reserve illustrating the six separate exclosures and outside area where experiments were also conducted. The five exclosures relevant to this study are named.

present, but quolls were excluded by an electrified fence. Our quoll-exposed treatment was the other three feral-free enclosures (First, Second, Northern Expansions totalling 4600 ha). The cat-exposed treatment, areas outside the reserve where feral cats, foxes and rabbits were present and reintroduced marsupials were absent (except occasionally dispersing quolls, Manning et al., 2022), was only used for hopping mice experiments. Rainfall and habitat are similar across the reserve, consisting of longitudinal sand dunes supporting *Acacia* and *Dodonaea* shrubland, clay interdunal swales with chenopod shrubland and mulga, *Acacia aneura*, sand plains (Munro et al., 2009).

Experimental Approach

Bettongs in the control and quoll-exposed treatments were first tested for general antipredator behaviour by quantifying measures of wariness and vigilance. Specifically, we tested trap docility (West et al., 2018), flight initiation distances (FID; Stankowich & Blumstein, 2005), and foraging behaviour. We then tested their specific responses to a range of predator and control stimuli by using food trays, scent and model experiments. We investigated specific reactions to quoll stimuli, representing a native predator, and then compared these to responses to cat stimuli, representing an introduced predator, and control stimuli including rabbit and artificial objects.

From May to July 2020, we cage-trapped, ear-tagged and fitted VHF radiocollars (25 g; Lotek Ltd., Havelock North, New Zealand) to 15 control bettongs (six females, nine males) and 14 quoll-exposed bettongs (11 females, three males). We did not capture hopping mice, but actively searched for popholes to first locate suitable sites to conduct experiments to quantify general vigilance and wariness. Similar to bettongs, food tray and model experiments were then also used to evaluate species-specific antipredator responses. Thirty-two active hopping mice popholes were found through active searching in dunes in each of our three treatment areas. All popholes used in experiments were at least 1 km from the edge of any treatment area as hopping mice can move through the 300 mm aperture netting fence and can travel up to 600 m in a single night within their home range (Bradley, 2009).

General Antipredator Behaviour

Bettongs

We scored trap behaviour of bettongs in both treatments to see whether docility changed with quoll exposure. We radiotracked collared individuals to burrows and set cage traps around burrows to trap the collared individuals. From May 2020 to March 2021, collared individuals were trapped one to three times, at least 4 months apart. During trapping, we scored behaviour of all bettongs while inside traps, including both collared bettongs and any conspecifics also caught at that burrow. We dichotomously scored whether animals moved in the trap, made noise, moved immediately from the trap into the capture bag when the trap door was opened and whether they moved in an agitated manner once secured in the bag, following West et al. (2018). Scores were summed and then subtracted from a total score of 4 to give a trap docility score where 0 = nondocile and 4 = docile (West, Blumstein, et al., 2019). To ensure individual scorers were consistent in their scoring, we trained together by scoring nonstudy bettongs prior to the first trapping event.

We measured FID once for each collared bettong in each treatment. Data were collected at least 1 week after collars were fitted to reduce the likelihood that trapping and collaring altered normal behaviour, following West et al. (2018). Briefly, each collared bettong was located at night using a VHF radio receiver. Working alone,

the scorer approached the bettong at a walking pace using a dim head torch until the animal fled and then the distance (m) before flight was initiated was measured with a handheld GPS unit. The same GPS unit was used for all scoring attempts to minimize error. If bettongs always stayed well ahead of the scorer (never seen) then the estimated minimum FID was recorded as the maximum distance that can be seen with the head torch, which was 40 m.

We quantified bettong foraging behaviour using food trays. Collared bettongs were radiotracked to their diurnal burrow and a food tray was placed 10 m (± 1 m) from the burrow. The food tray was a 10-litre plastic basin dug into the ground flush with the surface and filled with sand mixed with one cup of rolled oats to attract bettongs. A camera (Swift Enduro) was set 3 m from the food tray which recorded a 60 s video when triggered by motion (Appendix Fig. A1a). This was repeated every 6 months from May 2020 to June 2021 for all collared bettongs. Bettong foraging behaviour was quantified through an ethogram as described below.

Hopping mice

We quantified the GUD of seeds and general foraging behaviour of hopping mice by using an open versus cover experiment. Two seed trays (500 ml plastic tray) and two cameras were set up at each pophole, one 2 m from the pophole under a low-lying shrub (cover) and the other 2 m from the pophole in the opposite direction in the open (Appendix Fig. A1b). Each seed tray was placed inside a cage trap which was wired open with a wooden excluder at the entrance preventing larger mammals from entering. Each camera was set to record a 60 s video when triggered. Over 3 consecutive days, 30–40 g of sunflower seeds were mixed through sand placed inside each seed tray to attract hopping mice. Initially, 30 g of seed was used but later increased to 40 g as there were many hopping mice in some treatments. Each morning, the remaining seeds were collected and weighed to obtain the GUD for 3 consecutive days. A total of 10 popholes were used in each treatment, over a 6-day period, i.e. 2×3 -day blocks where five popholes in each treatment were visited each day.

Predator Recognition and Differentiation

The behavioural responses of bettongs to different predator (quoll: native predator; cat: introduced predator), nonpredator rabbit (introduced nonpredator) or control (water or novel object) stimuli were compared for each treatment. We used body odour, faeces and models of the above as stimuli in separate experiments (see below). Eight burrows were used in each treatment with a foraging tray placed at each burrow and a motion-activated camera (Swift Enduro) set 3 m from the food tray to record behaviour. Different stimuli were placed in or near each foraging tray each night and were randomized according to a Latin square design, so that each burrow received all four stimuli over a 4-night period.

Body odour

Body odour experiments used cotton towels that were placed in the bedding of captive quolls, rabbits and cats for 1 week, after which the towels were cut up into 10×10 cm pieces, placed in airtight containers and frozen until use. The cotton towels were collected from captive western quolls (Alice Springs Desert Park), household pet cats, domesticated European rabbits and a towel moistened with deionized water (control odour). The towels were attached to a stake and placed in the centre of the food tray in the afternoon of each experiment.

Faeces

Faecal samples were collected from household pet cats in addition to faeces within the colon of feral cats euthanized at the

Arid Recovery reserve. Rabbit and quoll faeces were collected from known rabbit warrens outside the reserve and quoll latrine sites inside the reserve. The faeces were mixed with water (1:1) inside a sealed container and then shaken to mix. Approximately 100 ml of this mixture, or 100 ml of water (control sand), was poured into a tub with 900 ml of sand and mixed through to imbue the sand with scent. We then spread 450 ml of scented or control sand evenly around each food tray.

Models

Models placed near food trays were used to test behavioural responses by both bettongs and hopping mice. Four types of models, with two replicates of each model, were used: two taxidermy western quolls (one prepared by Western Australian taxidermists and one prepared as part of this study), two taxidermy European rabbits and feral cats (which we made from locally caught and euthanized animals) and a 9-litre plastic bucket (control model). The models were placed 3 m from the food tray and a camera was placed on the opposite side, with the head of taxidermy models facing the camera.

Hopping mice

Predator recognition experiments for hopping mice were limited to model stimuli. A total of 32 popholes in each treatment were used for this experiment. Each night, for 8 nights, four popholes in each treatment were each randomly selected to receive a different model. The model and camera were placed 3 m from the seed tray, on the opposite side to the pophole, as described above. As in the open-cover experiment, each seed tray was placed inside a cage trap, wired open with a wooden excluder over the entrance. This experiment was only conducted for 1 night at each pophole, so the remaining seeds were collected in the morning and weighed to obtain the GUD for each pophole.

Video Analysis

Ethograms for each of the two species (Appendix Tables A1, A2) were adapted from similar studies (Morris et al., 2015; West et al., 2018) to score each video with the Behavioural Observation Research Interactive Software (BORIS; Friard et al., 2016). The behaviour of the first collared bettong that visited the tray was scored. If an uncollared bettong also visited the food tray, then the first video of an uncollared bettong was also scored. For hopping mice, the first 10 videos recorded at each site each night were used for video analysis. The behaviour of the first hopping mouse that visited the tray in each video was scored. Prior to scoring, all video files were renamed with a randomly generated number (1–1000) so that videos were scored blind. Not all visits were of equal length, so the proportion of time in sight was calculated for each animal (West et al., 2018). For bettongs, we analysed the proportion of time they were engaged in inattentive foraging (foraging head down only), and vigilance while foraging (pooled from the three head up/high behaviours), in addition to the number of vigilant head looks from time in sight. With a wide range of observable behaviours included in the ethogram (Appendix Table A1), it was difficult to quantify which were vigilant behaviours. However, inattentive foraging was easy to observe, so we assumed less time spent inattentive foraging meant more time spent being wary and aware. For hopping mice, we calculated the proportion of time each mouse was foraging at the tray and recorded latency to feed (minutes after sunset) for each video for each visit and was the number of visits to the food tray (per min) by each hopping mouse. The number of visits/min was used an index of wariness for each hopping mouse, as we assumed that if the hopping mice perceived the novel environment of a cage trap as unsafe it would make short, frequent trips inside the cage to grab seed and consume it outside the

cage. After removing videos with less than 10 s of video of animals on screen, we had 317 videos from the first visit by a bettong each night across all three predator recognition experiments, and 997 videos for both hopping mice experiments (Appendix Table A3).

Statistical Analysis

To test the effect of quoll exposure on trap docility and FID in bettongs we fitted generalized linear mixed models (GLMs) with a Poisson distribution. We included fixed effects of treatment (control/quoll-exposed), sex, an interaction between sex and treatment and a random effect of individual to account for multiple observations of each bettong for trap docility models.

We limited our behavioural analysis to videos only where bettongs were present for a minimum of 20 s, and for hopping mice a minimum of 10 s. For each behaviour we calculated the proportion of time from the total time each animal was present in the video. Models using behaviours scored as a proportion of time as the response were fitted with beta regression models as the length of the time an individual was visible was not consistent. For our response data from video analysis that were a measure of proportion of time, we used beta regression models as the length of time an individual was visible was not consistent. We transformed each proportion of time variable with equation (1) from Douma and Weedon (2019), to account for behaviours that were not recorded. We included fixed effects of treatment (control/quoll-exposed), stimuli (control, quoll, cat and rabbit) and an interaction between treatment and stimuli. We included precision terms of visit number (n^{th} animal to visit the tray each night), length of time on screen, whether conspecifics were present (yes/no) and for the bettong experiments, the order the stimuli were presented according to the Latin square design. To compare the rate of vigilant head looks and visits to the tray, we used the counts per video as our response variable and used GLMs with a negative binomial distribution. The time on screen was included as an offset. We used the same fixed effects and random terms as above for treatment and stimuli.

For hopping mice, we compared responses to different habitats and stimuli within each treatment, as ongoing monitoring across the Arid Recovery reserve indicated that hopping mice abundance varied between treatments (Appendix Fig. A2). To compare GUD values (amount (g) of seeds remaining) we fitted GLMs with a Poisson distribution. Our response variable for the GUD was a count variable and therefore we used a model with Poisson error distribution.

Statistical significance was set as $P < 0.05$ and all statistics were computed using R (version 4.1.1; R Core Team, PBC, Boston, MA, U.S.A.), using the packages betareg (Ferrari & Cribari-Neto, 2004), lmerTest (Zeileis & Hothorn, 2002) and glmmTMB (Brooks et al., 2017). When $0.05 < P < 0.1$, we have noted potential trends in the Results section. All plots show predicted estimated marginal means from the package emmeans (Lenth, 2020) and were plotted with ggplot2 (Wickham, 2016). Where the same bettong or burrow was used under repeated settings, we included bettong or burrow ID as a random effect in the relevant analyses and tested the importance of these variables using likelihood ratio tests (LRT). Model fits were checked visually by plotting residuals (using `sweighted2` residuals for beta regression models) and testing for overdispersion in the package DHARMA (Hartig, 2020).

Ethical Note

Ethics approval was obtained from the University of New South Wales Animal Care and Ethics Committee; approval no. 20/109A. No bettongs or mice were harmed during these procedures.

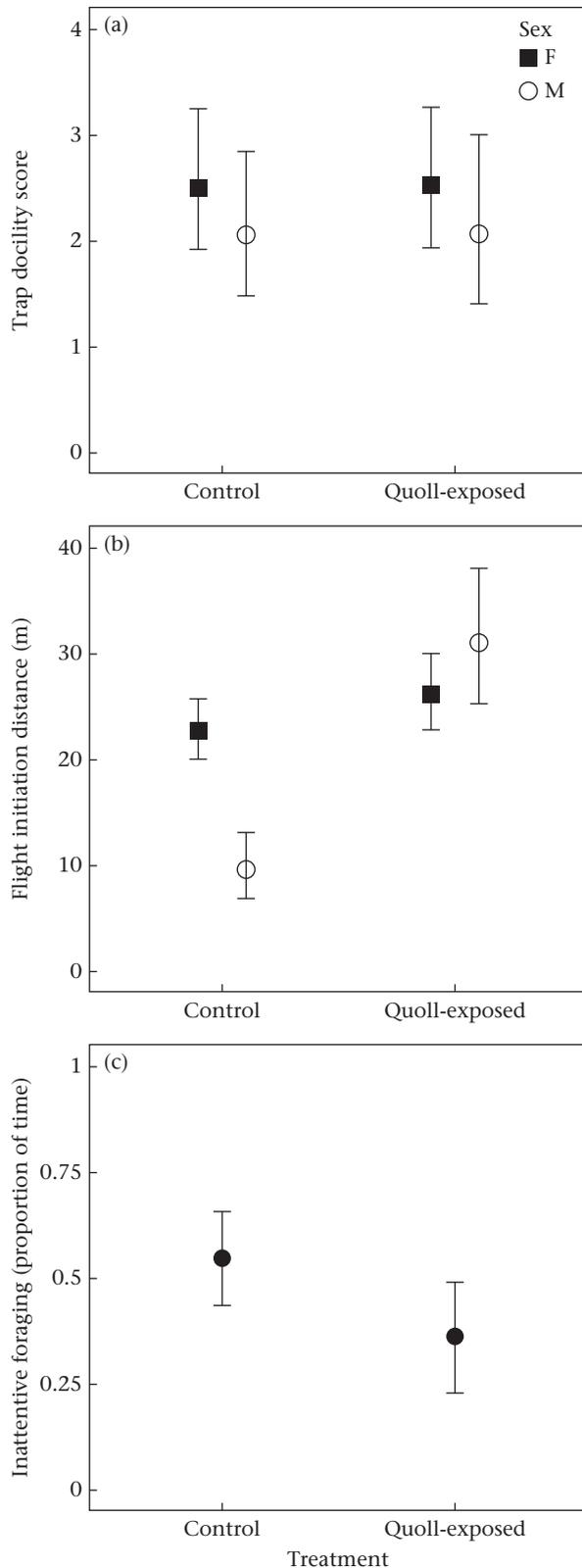


Figure 2. (a) Mean trap docility scores for bettongs grouped by sex, (b) mean flight initiation distances for bettongs grouped by sex (F: female; M: male) and (c) predicted proportion of time spent in inattentive foraging by bettongs at foraging trays in control and quoll-exposed treatments. Bars are 95% confidence intervals.

Bettongs were live trapped as previously described (Harrison et al., 2023; West et al., 2018). Twenty-nine bettongs (17 females, 12 males) had radiocollars put on them; trap docility scores were conducted on 58 occurrences on 40 individual bettongs (27 females, 13 males); and FIDs were conducted on 26 bettongs (19 females, seven males). Traps were baited with a combination of peanut butter and rolled oats before sunset and set on nights without excessive temperature ($>30^{\circ}\text{C}$) and were checked no more than 2 h after sunrise. Bettongs were transferred from cage traps into a dark nylon fleece bag, for processing and/or collar attachment. If bettongs were to be collared, they were held overnight indoors in a pet pack, provided with food and water and released the following evening. If not required for collaring, they were released in the field after processing at the site of capture. Collars weighed 3% of an 830 g subadult bettong; all bettongs were heavier than this when collared. To ensure animal movements were not hindered by the capture and processing procedure, daily radio-tracking of individuals commenced immediately after collar attachment for the first week, followed by weekly checks for 3 months. Each collared bettong was trapped every few months and checked for signs of rubbing or cuts (we removed one collar because of chafing). Collars were loosened if an animal had gained weight. All collars were removed in June 2021.

Hopping mice were not captured, and we have no reason to believe our experiments created any welfare issues. We conducted two experiments involving foraging trays, where cage traps were securely wired open and a wooden excluder wired around the door to prevent larger mammals entering the cage traps, as the foraging trays were located inside. We placed trays and traps near 60 hopping mice popholes for the first experiment (open versus cover) and at 120 popholes for the second experiment (models). Hopping mice were free to enter and leave the traps and foraging trays at will. No mice were deliberately or inadvertently captured or harmed by cage traps and all mice were able to access their popholes freely.

RESULTS

Bettongs

There was no difference in trap docility scores between control ($N = 32$: 19 females, 13 males) and quoll-exposed ($N = 26$: 19 females, seven males) bettongs (GLM: $\beta = 0.004$, $z = 0.03$, $P = 0.98$) or between the sexes (GLM: $\beta = -0.20$, $z = -1.05$, $P = 0.30$; Fig. 2a). However, male quoll-exposed bettongs ($N = 3$) were flightier and more responsive with higher FID scores than control males (GLM: $N = 4$, $\beta = 1.04$, $z = 4.85$, $P < 0.0001$; Fig. 2b). In comparison, there was no difference in female FIDs ($N = 11$ control, eight quoll-exposed) between treatments (GLM: $\beta = -0.14$, $z = -1.53$, $P = 0.13$; Fig. 2b). At foraging trays, quoll-exposed bettongs ($N = 17$) spent less time engaged in inattentive foraging behaviour than control bettongs (beta regression: $N = 27$, $\beta = -0.77$, $z = -2.055$, $P = 0.040$; Fig. 2c). There were no differences for other behaviours scored from video analysis (Appendix Fig. A3a–c).

Across each of the three predator recognition experiments, bettongs in both treatments spent similar time engaged in inattentive foraging (more time head down) when exposed to the control stimuli (Fig. 3a–c). However, quoll-exposed bettongs spent less time in inattentive foraging in response to all body odour scents (beta regression: rabbit: $\beta = 0.33$, $z = 3.29$, $P = 0.001$; quoll: $\beta = 0.23$, $z = 2.29$, $P = 0.02$; cat: $\beta = 0.38$, $z = 3.63$, $P = 0.0003$; Fig. 3a) than control bettongs. In the body odour experiment, the

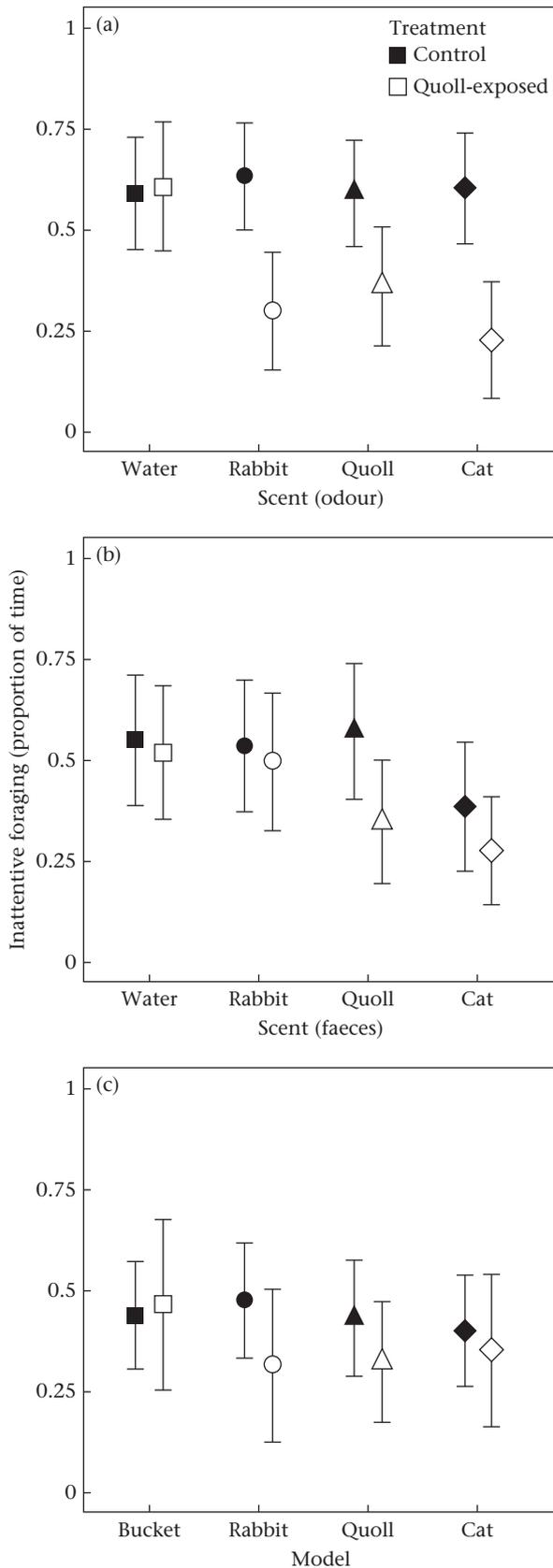


Figure 3. Predicted proportion of time spent by bettongs in inattentive foraging at foraging trays in experiments in which (a) body odour, (b) faeces or (c) models of a control, a non-native nonpredator (rabbit), a native predator (quoll) or a non-native predator (cat) were present. Bars are 95% confidence intervals.

order of stimuli was important, with greater time spent in inattentive foraging by the third and fourth consecutive night a tray with scent was placed near their burrow (beta regression: night 3: $\beta = 0.76$, $z = 2.19$, $P = 0.028$; night 4: $\beta = 1.15$, $z = 3.34$, $P = 0.0008$). In the scent experiment, when comparing quoll-exposed to control bettongs, quoll-exposed bettongs tended to spend less time in inattentive foraging when presented with quoll or cat faeces compared with rabbit faeces and water; however, this did not reach our significance threshold and was only significant when comparing responses to cat faeces (beta regression: water–cat: $\beta = -0.24$, $z = -2.26$, $P = 0.024$; rabbit–cat: $\beta = -0.22$, $z = -1.99$, $P = 0.046$; water–quoll: $\beta = -0.17$, $z = -1.51$, $P = 0.13$; rabbit–quoll: $\beta = -0.15$, $z = -1.28$, $P = 0.20$; Fig. 3b). However, control bettongs also spent less time inattentive in response to the cat faeces, but this was not significant (beta regression: $\beta = -0.16$, $z = -1.41$, $P = 0.16$; Fig. 3b). When comparing the response of quoll-exposed and control bettongs to quoll faeces, quoll-exposed bettongs tended to spend less time in inattentive foraging; however, this did not reach our significance threshold (beta regression: $\beta = 0.22$, $z = 1.94$, $P = 0.053$; Fig. 3b). Control and quoll-exposed bettongs did not differ in time spent in inattentive foraging for any of the models in the model experiment (Fig. 3c), nor were there any significant differences in the other behaviours displayed by bettongs in the three experiments (Appendix Figs A4–A6).

Spinifex Hopping Mice

Predator-exposed hopping mice displayed increased wariness (more visits) at trays in open habitat compared to those in cover; however, they did not reach our significance threshold (GLM: quoll-exposed: $\beta = 0.25$, $z = 1.80$, $P = 0.07$; cat-exposed: $\beta = 0.26$, $z = 1.68$, $P = 0.09$; Fig. 4a). Quoll-exposed hopping mice consumed more food under cover than in the open (GLM: $\beta = 0.55$, $z = 3.14$, $P = 0.002$), whereas there was no difference in GUD values between habitats for cat-exposed hopping mice (GLM: $\beta = -0.02$, $z = -0.15$, $P = 0.885$; Fig. 4b). Control hopping mice tended to consume more food in open habitats; however, this did not reach our significance threshold (GLM: $\beta = -0.54$, $z = -1.74$, $P = 0.08$; Fig. 4b). Hopping mice within each treatment spent similar amounts of time foraging in each habitat (beta regression: $\beta = 0.20$, $z = 0.99$, $P = 0.32$; Appendix Fig. A7a); however, cat-exposed hopping mice took longer to approach and feed in covered habitats (GLM: $\beta = 0.25$, $z = 2.54$, $P = 0.01$; Appendix Fig. A7b).

Control hopping mice did not discriminate between predator models in terms of wariness (visits/min); however, predator-exposed hopping mice reacted differently to the models of predators to which they were exposed. Quoll-exposed hopping mice were more wary when the quoll model was present (GLM: $\beta = 0.37$, $z = 2.24$, $P = 0.026$) and cat-exposed hopping mice were more wary when the cat model was present (GLM: $\beta = 0.49$, $z = -2.77$, $P = 0.006$), compared to the buckets (Fig. 4c). Control hopping mice were less wary (fewer visits) when comparing predator models to the bucket (GLM: quoll: $\beta = -0.44$, $z = -2.89$, $P = 0.004$; cat: $\beta = -0.41$, $z = -2.78$, $P = 0.006$; Fig. 4c).

Control and cat-exposed hopping mice consumed similar amounts of food, regardless of the type of model present (Fig. 4d). However, when compared to the control, quoll-exposed hopping mice consumed less food when exposed to the models of the rabbit (GLM: $\beta = -0.29$, $z = -2.75$, $P = 0.006$) and cat (GLM: $\beta = -0.26$, $z = -3.04$, $P = 0.002$; Fig. 4d). Control and quoll-exposed hopping mice spent similar proportions of time foraging in the presence of each model; however, cat-exposed hopping mice foraged longer with the cat model compared to the control (beta regression: $\beta = 0.16$, $z = 3.09$, $P = 0.002$; Appendix Fig. A7c).

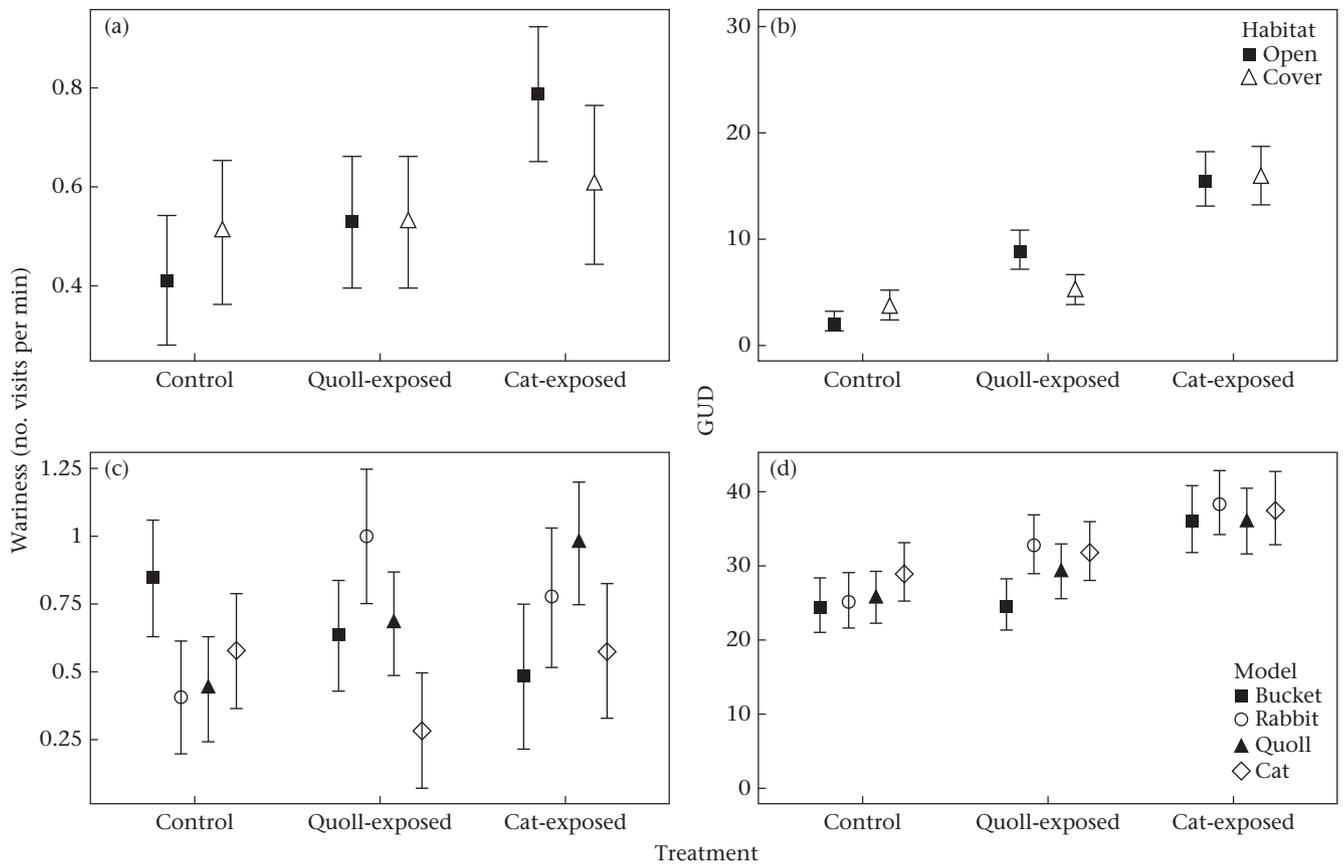


Figure 4. Responses of control, quoll- or cat-exposed spinifex hopping mice at foraging trays (a, b) in open and covered habitats and (c, d) with different models (a control, non-native nonpredator (rabbit), a native predator (quoll) or a non-native predator (cat)): (a, c) wariness (number of visits/min to food tray); (b, d) GUD (g seeds remaining) values. Bars are 95% confidence intervals.

DISCUSSION

Predator avoidance behaviours in both prey species increased once quolls were reintroduced. Quoll-exposed bettongs were warier and more vigilant, while quoll-exposed hopping mice perceived greater risk of predation when foraging in open habitats, and with models. While predator recognition varied between stimuli and treatment, changes in foraging behaviour between predator exposed and control prey animals demonstrate that reintroducing predators can trigger changes in behaviour in as little as 2 years.

Quoll-exposed bettongs responded similarly to bettongs exposed to cats in a previous study at the reserve (Moseby et al., 2022; West et al., 2018), with predator-exposed bettongs fleeing earlier when approached and exhibiting increased wariness compared to control bettongs. However, exposure to quolls did not result in some reactions documented in cat-exposed bettongs, such as increased trap docility or slow food tray approach (West et al., 2018). Increased wariness after quoll exposure has previously been documented in this reserve, with quoll-exposed greater bilbies, *Macrotis lagotis*, spending more time under cover (Van der Weyde et al., 2023) and Shark Bay bandicoots, *Perameles bougainville*, exhibiting longer flight initiation distances (Waaleboer et al., 2024) compared to control populations. While other populations of spinifex hopping mice (where native mammalian predators are absent) primarily forage in open habitats and rely on escape rather than avoidance when encountering predators (Spencer et al., 2014b), quoll-exposed hopping mice primarily foraged under

cover, indicating that they might not be able to rely on escape to avoid quoll predation. Other native rodents also primarily forage under cover in response to high cat activity (Gordon et al., 2015). Some mammal species are able to differentiate between predator and nonpredator models (Blumstein et al., 2000), and this was apparent in quoll-exposed hopping mice with GUD values. The GUD values reflected the different levels of hopping mice activity in each treatment (Appendix Fig. A2). Our results support other studies that have recorded changes in (native) prey behaviour in response to quoll exposure. Exposure to northern quolls, *Dasyurus hallucatus*, resulted in increased shyness, predator scent aversion and lower foraging rates in a population of small rodents (Jolly et al., 2021). Consequently, we are confident that exposure to quolls has resulted in changes in antipredator responses to the hopping mice population in this fenced reserve.

Exposing reintroduced prey to quolls can act as a mechanism to teach appropriate responses to novel predators, such as feral cats (Van der Weyde et al., 2023), by improving general wariness. However, although exposing both species to quolls improved their antipredator behaviours, we found only limited evidence that predator recognition is transferred to novel predators. Quoll-exposed bettongs were more wary in response to both quoll and cat faeces and body odour, but this was also recorded for rabbit body odour suggesting the response was due to novelty rather than predator discrimination. Additionally, control bettongs also tended to respond to cat faeces, suggesting this response may not have been driven by quoll exposure or that faeces is not a suitable cue to use in predator awareness studies possibly because of evolutionary

avoidance of pathogens (Doherty & Ruehle, 2020). More research and larger sample sizes are needed to determine whether exposure to native predators can improve novel predator recognition. Hopping mice showed an appropriate predator-specific reaction to quolls or cats consistent with their prior exposure but did not transfer this behaviour to other predator species. Studies have reported mixed responses for the ability of rodents to distinguish between novel and native predators (Carthey & Banks, 2016; Banks et al., 2018; Wallach et al., 2022), and our results suggest that behavioural responses to predators may be specific to each predator species rather than a predator archetype. It is possible the short reproductive cycles of spinifex hopping mice (Breed, 1979; Crichton, 1974) compared to bettongs (Short & Turner, 1999) helped accelerate their response to cats and quolls. In addition, their smaller size makes hopping mice a more obtainable prey item for a greater range of predatory species (Preisser & Orrock, 2012) and therefore they might display more generalized antipredator responses.

Exposing prey to native predators may prepare threatened prey species to coexist with novel predators in large, fenced reserves. If prey populations are sufficiently large when a native predator species is reintroduced, those individuals that survive initial exposure to it and then coexist with it for several generations could become predator savvy (Wallach et al., 2022). However, if the ultimate goal is to reintroduce prey to unfenced areas that contain novel predators (Butler et al., 2019; Miritis et al., 2020; Moseby et al., 2012, 2019), direct exposure to live feral predators in low densities may, for some species, be the best option to accelerate the selection of antipredator responses specific to novel predators (Blumstein et al., 2019; Gérard et al., 2014; Moseby et al., 2018a; West et al., 2018).

Exposure to complex predator stimuli in this study demonstrates that different prey species can vary considerably in their responses to the same predators (Van der Weyde et al., 2023). We could also have used a native nonpredator as an extra stimulus, but we were constrained by a low sample size and thus limited our analysis to four stimuli (control, native predator, novel predator and novel nonpredator). Although we used multiple types of stimuli, testing for recognition and discrimination by prey species to different predators was difficult. Assessing neophobic responses may be more useful than the methods presented here to measure changes in boldness between populations and to compare findings with those of other studies measuring behaviour after the introduction of a predator (Harrison et al., 2021; Jolly et al., 2021; Van der Weyde et al., 2023). Alternatively, one could use high-risk stimuli such as a approach distances (FIDs) and trap behaviour scores (the stimulus being a human approaching an animal), which may be more likely to elicit a response than passive stimuli such as odour in behavioural trials (Moseby et al., 2024). A final limitation of our study was that bettong sample sizes were unexpectedly low after a population decline due to a multiyear drought (Moseby et al., 2022, 2023).

Reintroducing native predators to fenced reserves may address issues of prey naiveté in addition to conserving the predators themselves. The reintroduction of quolls to this reserve resulted in documented changes to the behaviour of two prey species, supporting previous research documenting behaviour changes in other species. Exposure to native predators increased general wariness which may help improve survival when releasing animals into environments with novel predators. We also found weak evidence that exposure to native predators improved predator reactions towards novel predators (through olfactory cues). Testing whether

exposure to native predators can be used as a stepping stone to coexistence with novel predators would require releasing quoll-exposed and control animals into areas where feral predators were present and comparing survival (as has been attempted in other studies, see Van der Weyde et al., 2023). Predator discrimination may not be important for survival if general wariness is sufficient to avoid predation by native and novel predators. We have shown here that positive outcomes for both native predators and prey can be triggered by the reintroduction of native predators and recommend further research into these processes under different conditions.

Author Contributions

Mike Letnic: Funding acquisition, Methodology, Writing—review & editing. **Graeme Finlayson:** Funding acquisition, Supervision, Writing—original draft, Writing—review & editing. **Katherine E Moseby:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing—original draft, Writing—review & editing. **Daniel T Blumstein:** Methodology, Validation, Writing—original draft, Writing—review & editing. **Leanne K Van der Weyde:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Visualization, Writing—original draft, Writing—review & editing. **Ben Stepkovitch:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing—original draft, Writing—review & editing

Data Availability

Data are available from the Mendeley Data repository: <https://doi.org/10.17632/dcnbh2xnx4.2>.

Declaration of Interest

None.

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References

- Banks, P., Carthey, A., & Bytheway, J. P. (2018). Australian native mammals recognize and respond to alien predators: A metaanalysis. *Proceedings of the Royal Society B: Biological Sciences*, 285(1885). <https://doi.org/10.1098/rspb.2018.0857>
- Bannister, H. L., Letnic, M., Blumstein, D. T., & Moseby, K. E. (2021). Individual traits influence survival of a reintroduced marsupial only at low predator densities. *Animal Conservation*. <https://doi.org/10.1111/acv.12690>

- Bannister, H. L., Lynch, C. E., & Moseby, K. E. (2016). Predator swamping and supplementary feeding do not improve reintroduction success for a threatened Australian mammal, *Bettongia lesueur*. *Australian Mammalogy*, 38(2), 177–187.
- Bedoya-Perez, M., Carthey, A., Mella, V., McArthur, C., & Banks, P. (2013). A practical guide to avoid giving up on giving-up densities. *Behavioral Ecology and Sociobiology*, 67(10), 1541–1553. <https://doi.org/10.1007/s00265-013-1609-3>
- Berger, J., Swenson, J. E., & Persson, I.-L. (2001). Recolonizing carnivores and naïve prey: Conservation lessons from Pleistocene extinctions. *Science*, 291(5506), 1036–1039. <https://doi.org/10.1111/cobi.12415>
- Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L., & Gaston, K. J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science*, 305(5692), 1955–1958.
- Blumstein, D. T., & Daniel, J. C. (2005). The Loss of anti-predator behaviour following isolation on islands. *Proceedings: Biological Sciences*, 272(1573), 1663–1668. <https://doi.org/10.1098/rspb.2005.3147>
- Blumstein, D. T., Daniel, J. C., Griffin, A. S., & Evans, C. S. (2000). Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behavioral Ecology*, 11(5), 528–535.
- Blumstein, D. T., Letnic, M., & Moseby, K. (2019). In situ predator conditioning of naïve prey prior to reintroduction. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 374(1781). <https://doi.org/10.1098/rstb.2018.0058>
- Bradley, C. E. (2009). The socio-ecology of two species of Australian native rodent-*Notomys mitchelli* and *Notomys alexis* [PhD thesis]. University of Adelaide.
- Breed, W. (1979). The reproductive rate of the hopping-mouse *Notomys alexis* and its ecological significance. *Australian Journal of Zoology*, 27(2), 177–194.
- Breed, W. G. (1998). Spinifex hopping mouse *Notomys alexis* (Thomas, 1922). In R. Strahan (Ed.), *The mammals of Australia. The national photographic index of Australian wildlife* (pp. 568–570). Reed New Holland.
- Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., ... Bolker, B. M. (2017). glimmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal*, 9(2), 378–400. <https://doi.org/10.32614/RJ-2017-066>
- Butler, K., Paton, D., & Moseby, K. E. (2019). One-way gates successfully facilitate the movement of burrowing bettongs (*Bettongia lesueur*) through exclusion fences around reserve. *Austral Ecology*, 44(2), 199–208. <https://doi.org/10.1111/aec.12664>
- Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. *Biological Reviews*, 89(4), 932–949. <https://doi.org/10.1111/brv.12087>
- Carthey, A. J., & Banks, P. B. (2016). Naïveté is not forever: Responses of a vulnerable native rodent to its long term alien predators. *Oikos*, 125(7), 918–926.
- Carthey, A. J., & Blumstein, D. T. (2018). Predicting predator recognition in a changing world. *Trends in Ecology & Evolution*, 33(2), 106–115.
- Christensen, P., & Burrows, N. (1995). Project desert dreaming: Experimental reintroduction of mammals to the Gibson desert, Western Australia. In M. Serena (Ed.), *Reintroduction Biology of Australian New Zealand Fauna* (pp. 199–207) (Surrey Beatty).
- Cox, J. G., & Lima, S. L. (2006). Naïveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution*, 21(12), 674–680.
- Crichton, E. G. (1974). Aspects of reproduction in the genus *Notomys* (Muridae). *Australian Journal of Zoology*, 22(4), 439–447.
- Cunningham, C. X., Johnson, C. N., Hollings, T., Kreger, K., & Jones, M. E. (2019). Trophic rewilding establishes a landscape of fear: Tasmanian devil introduction increases risk-sensitive foraging in a key prey species. *Ecography*, 42(12), 2053–2059.
- Doherty, J.-F., & Ruehle, B. (2020). An integrated landscape of fear and disgust: The evolution of avoidance behaviors amidst a myriad of natural enemies. *Frontiers in Ecology and Evolution*, 8, Article 564343.
- Douma, J. C., & Weedon, J. T. (2019). Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. *Methods in Ecology and Evolution*, 10(9), 1412–1430. <https://doi.org/10.1111/2041-210X.13234>
- Ferrari, S., & Cribari-Neto, F. (2004). Beta regression for modelling rates and proportions. *Journal of Applied Statistics*, 31(7), 799–815.
- Friard, O., Gamba, M., & Fitzjohn, R. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11), 1325–1330. <https://doi.org/10.1111/2041-210X.12584>
- Gérard, A., Jourdan, H., Cugnière, C., Millon, A., & Vidal, E. (2014). Is naïveté forever? Alien predator and aggressor recognition by two endemic island reptiles. *Naturwissenschaften*, 101, 921–927.
- Glen, A. S., & Dickman, C. R. (2005). Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews*, 80(3), 387–401. <https://doi.org/10.1017/S1464793105006718>
- Gordon, C. E., Feit, A., Grüber, J., & Letnic, M. (2015). Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proceedings of the Royal Society B: Biological Sciences*, 282(1802), Article 20142870.
- Harrison, N. D., Phillips, B. L., Hemmi, J. M., Wayne, A. F., Steven, R., & Mitchell, N. J. (2021). Identifying the most effective behavioural assays and predator cues for quantifying anti-predator responses in mammals: A systematic review protocol. *Environmental Evidence*, 10(1), 1–9.
- Harrison, N. D., Phillips, B. L., Mitchell, N. J., Wayne, J. C., Maxwell, M. A., Ward, C. G., & Wayne, A. F. (2023). Perverse outcomes from fencing fauna: Loss of anti-predator traits in a havened mammal population. *Biological Conservation*, 281, Article 110000.
- Hartig, F. (2020). DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.2.0. Retrieved 01/07/2020 from <https://CRAN.R-project.org/package=DHARMA>.
- Jolly, C., Smart, A., Moreen, J., Webb, J., Gillespie, G., & Phillips, B. (2021). Trophic cascade driven by behavioural fine-tuning as naïve prey rapidly adjust to a novel predator. *Ecology*, 102(7), Article e03363. <https://doi.org/10.1101/856997>
- Jolly, C. J., Webb, J., & Phillips, B. (2018). The perils of paradise: An endangered species conserved on an island loses antipredator behaviours within 13 generations. *Biological Letters*, 14(6). <https://doi.org/10.1098/rsbl.2018.0222>
- Legge, S., Woinarski, J. C. Z., Burbidge, A. A., Palmer, R., Ringma, J., Radford, J. Q., ... Tuft, K. (2018). Havens for threatened Australian mammals: The contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. *Wildlife Research*, 45(7), 627–644. <https://doi.org/10.1071/WR17172>
- Lenth, R. (2020). emmeans: estimated marginal means, aka least-square means. R package version 1.5.0. Retrieved 01/07/2020 from Available from: <https://CRAN.R-project.org/package=emmeans>.
- Lewis, S. E., Sloss, C. R., Murray-Wallace, C. V., Woodroffe, C. D., & Smithers, S. G. (2013). Post-glacial sea-level changes around the Australian margin: A review. *Quaternary Science Reviews*, 74, 115–138.
- Makin, D. F., Chamailé-Jammes, S., & Shrader, A. M. (2018). Changes in feeding behavior and patch use by herbivores in response to the introduction of a new predator. *Journal of Mammalogy*, 99(2), 341–350. <https://doi.org/10.1093/jmammal/gyx177>
- Manning, T. P., Austin, J. J., Moseby, K. E., & Jensen, M. A. (2022). Skewed paternity impacts genetic diversity in a small reintroduced population of western quolls (*Dasyurus geoffroii*). *Australian Mammalogy*. <https://doi.org/10.1071/AM22012>
- Miritis, V., Rendall, A. R., Doherty, T. S., Coetsee, A. L., & Ritchie, E. G. (2020). Living with the enemy: A threatened prey species coexisting with feral cats on a fox-free island. *Wildlife Research*, 47(8), 633–642.
- Morris, S. D., Brook, B. W., Moseby, K. E., & Johnson, C. N. (2021). Factors affecting success of conservation translocations of terrestrial vertebrates: A global systematic review. *Global Ecology and Conservation*, 28, Article e01630.
- Morris, T., Gordon, C. E., & Letnic, M. (2015). Divergent foraging behaviour of a desert rodent, *Notomys fuscus*, in covered and open microhabitats revealed using giving up densities and video analysis. *Australian Mammalogy*, 37(1), 46. <https://doi.org/10.1071/AM14030>
- Moseby, K. E., Blumstein, D. T., Letnic, M., Trenwith, B., & Van der Weyde, L. K. (2024). Novel use of a common environment experiment to test for persistent changes in anti-predator behaviour after exposure to live predator (Submitted manuscript).
- Moseby, K. E., Cameron, A., & Crisp, H. (2012). Can predator avoidance training improve reintroduction outcomes for the greater bilby in arid Australia? *Animal Behaviour*, 83(4), 1011. <https://doi.org/10.1016/j.anbehav.2012.01.023>
- Moseby, K. E., Hill, B. M., & Read, J. L. (2009). Arid Recovery – a comparison of reptile and small mammal populations inside and outside a large rabbit, cat and fox-proof enclosure in arid South Australia. *Austral Ecology*, 34(2), 156–169. <https://doi.org/10.1111/j.1442-9993.2008.01916.x>
- Moseby, K., Letnic, M., Blumstein, D. T., & West, R. (2018a). Designer prey: Can controlled predation accelerate selection for anti-predator traits in naïve populations? *Biological Conservation*, 217(C), 213–221. <https://doi.org/10.1016/j.biocon.2017.09.022>
- Moseby, K., Letnic, M., Blumstein, D. T., & West, R. (2019). Understanding predator densities for successful co-existence of alien predators and threatened prey. *Austral Ecology*, 44(3), 409–419. <https://doi.org/10.1111/aec.12697>
- Moseby, K., Lollback, G. W., & Lynch, C. E. (2018b). Too much of a good thing; successful reintroduction leads to overpopulation in a threatened mammal. *Biological Conservation*, 219, 78–88. <https://doi.org/10.1016/j.biocon.2018.01.006>
- Moseby, K., & Read, J. (2006). The efficacy of feral cat, fox and rabbit exclusion fence designs for threatened species protection. *Biological Conservation*, 127(4), 429–437.
- Moseby, K., Read, J. L., Paton, D. C., Copley, P., Hill, B. M., & Crisp, H. A. (2011). Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation*, 144(12), 2863–2872. <https://doi.org/10.1016/j.biocon.2011.08.003>
- Moseby, K., Read, J., Tuft, K., & Van der Weyde, L. (2023). Influence of interactive effects on long-term population trajectories in multispecies reintroductions. *Conservation Biology*. <https://doi.org/10.1111/cobi.14209>

- Moseby, K., Van der Weyde, L., Letnic, M., Blumstein, D. T., West, R., & Bannister, H. (2022). Addressing prey naivety in native mammals by accelerating selection for antipredator traits. *Ecological Applications*, Article e2780.
- Munro, N. T., Moseby, K. E., & Read, J. L. (2009). The effects of browsing by feral and re-introduced native herbivores on seedling survivorship in the Australian rangelands. *Rangeland Journal*, 31(4), 417. <https://doi.org/10.1071/RJ08027>
- Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Marasini, G. G., ... Rondinini, C. (2013). Generation length for mammals. *Nature Conservation*, 5, 89–94.
- Paltridge, R., Gibson, D., & Edwards, G. (1997). Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research*, 24(1), 67–76.
- Preisser, E. L., & Orrock, J. L. (2012). The allometry of fear: Interspecific relationships between body size and response to predation risk. *Ecosphere*, 3(9), 1–27.
- Radford, J. Q., Woinarski, J. C., Legge, S., Baseler, M., Bentley, J., Burbidge, A. A., ... Dickman, C. R. (2018). Degrees of population-level susceptibility of Australian terrestrial non-volant mammal species to predation by the introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*). *Wildlife Research*, 45(7), 645–657.
- Read, J., & Bowen, Z. (2001). Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildlife Research*, 28(2), 195–203.
- Ross, A. K., Letnic, M., Blumstein, D. T., & Moseby, K. E. (2019). Reversing the effects of evolutionary prey naivety through controlled predator exposure. *Journal of Applied Ecology*, 56(7), 1761–1769. <https://doi.org/10.1111/1365-2664.13406>
- Salo, P., Korpimäki, E., Banks, P., Nordstrom, M., & Dickman, C. R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B: Biological Sciences*, 274(1615), 1237–1243. <https://doi.org/10.1098/rspb.2006.0444>
- Short, J., & Turner, B. (1999). Ecology of burrowing bettongs, *Bettongia lesueur* (Marsupialia: Potoroidae), on Dorre and Bernier islands, western Australia. *Wildlife Research*, 26(5), 651–669.
- Short, J., & Turner, B. (2000). Reintroduction of the burrowing bettong *Bettongia lesueur* (Marsupialia: Potoroidae) to mainland Australia. *Biological Conservation*, 96(2), 185–196. [https://doi.org/10.1016/S0006-3207\(00\)00067-7](https://doi.org/10.1016/S0006-3207(00)00067-7)
- Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., ... Vonesh, J. R. (2010). Predator–prey naivety, antipredator behavior, and the ecology of predator invasions. *Oikos*, 119(4), 610–621. <https://doi.org/10.1111/j.1600-0706.2009.18039.x>
- Spencer, E. E., Crowther, M. S., & Dickman, C. R. (2014a). Diet and prey selectivity of three species of sympatric mammalian predators in central Australia. *Journal of Mammalogy*, 95(6), 1278–1288.
- Spencer, E. E., Crowther, M. S., & Dickman, C. R. (2014b). Risky business: Do native rodents use habitat and odor cues to manage predation risk in Australian deserts? *PLoS One*, 9(2), Article e90566.
- Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), 2627–2634.
- Stepkovitch, B., Kingsford, R. T., & Moseby, K. E. (2022). A comprehensive review of mammalian carnivore translocations. *Mammal Review*, 52(4), 554–572. <https://doi.org/10.1111/mam.12304>
- Stepkovitch, B., Neave, G., Jensen, M., Tuft, K., & Moseby, K. E. (2023). From threatened to threatening: Impacts of a reintroduced predator on reintroduced prey. *Animal Conservation*. <https://doi.org/10.1111/acv.12920>
- Tay, N. E., Fleming, P. A., Warburton, N. M., & Moseby, K. E. (2021). Predator exposure enhances the escape behaviour of a small marsupial, the burrowing bettong. *Animal Behaviour*, 175, 45–56.
- Thompson, G. G., & Thompson, S. (2007). Are backfilled burrows a predator protection strategy for the Spinifex Hopping Mouse. *Journal of the Royal Society of Western Australia*, 90, 111–113.
- Van der Weyde, L. K., Blumstein, D. T., Letnic, M., Tuft, K., Ryan-Schofield, N., & Moseby, K. E. (2023). Can native predators be used as a stepping stone to reduce prey naivety to novel predators? *Behavioral Ecology*, 34(1), 63–75.
- Waaleboer, J. M., Van der Weyde, L. K., & Moseby, K. E. (2024). Rapid change in antipredator behaviour of a threatened marsupial after thousands of years of isolation from predators. *Austral Ecology*, 49(2), Article e13484.
- Wallach, A. D., Ramp, D., Benítez-López, A., Wooster, E. I., Carroll, S., Carthey, A. J., ... Svenning, J.-C. (2022). Savviness of prey to introduced predators. *Conservation Biology*, 37(2), Article e14012. <https://doi.org/10.1111/cobi.14012>
- Watts, C. H. S., & Aslin, H. J. (1981). *The rodents of Australia*. Angus & Robertson.
- West, R. S., Blumstein, D. T., Letnic, M., & Moseby, K. (2019a). Searching for an effective pre-release screening tool for translocations: Can trap temperament predict behaviour and survival in the wild? *Biodiversity & Conservation*, 28(1), 229–243. <https://doi.org/10.1007/s10531-018-1649-0>
- West, R. S., Letnic, M., Blumstein, D. T., & Moseby, K. E. (2018). Predator exposure improves anti-predator responses in a threatened mammal. *Journal of Applied Ecology*, 55(1), 147–156. <https://doi.org/10.1111/1365-2664.12947>
- West, R. S., Tilley, L., & Moseby, K. E. (2019b). A trial reintroduction of the western quoll to a fenced conservation reserve: Implications of returning native predators. *Australian Mammalogy*, 42(3), 257–265. <https://doi.org/10.1071/AM19041>
- Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. Springer-Verlag. <https://ggplot2.tidyverse.org>.
- Zeileis, A., & Hothorn, T. (2002). Diagnostic checking in regression relationships. *R News*, 2, 7–10.

Appendix

Table A1

Ethogram of behaviours for bettongs visiting food trays indicating the behaviours included in each of the behavioural categories analysed

Behaviour	Description
Approach	
Fast approach	Hops rapidly towards tray without pausing
Slow approach	Hops slowly and tentatively towards tray pausing and looking up (including at model) or slowly approaches tray quadrupedally
No approach	Present but does not approach tray
Foraging	
Inattentive	Head down and foraging
Head mid-up	Head up mid-way, chewing and looking around
Head high-chewing	Head up high, pausing, but still chewing
Head high-vigilant	Head up looking, no chewing
Leave	
Fast leave	Hops rapidly from tray
Slow leave	Hops slowly from tray, stopping and pausing at times
Interactions	
Conspecific	Looking at other bettongs
Interspecific	Looking at other species
Fighting	Aggressive interaction with another bettong, or harassing/being harassed
Unknown	Looking at something but unknown
Model	Interacting (grabbing/sniffing/chewing etc.) with model* or towel
Sniffing	
Hop-sniff	Hops and stops to sniff air (bipedal)
Quad-sniff	Moves quadrupedally and stops to sniff ground
Tray-sniff	Sniffs tray (at/in tray)
Towel-sniff	Sniffs scent towel
Sand-sniff	Sniffs scented sand around bowl
Camera-sniff	Sniffs camera
Visual	
Out of sight	Out of sight of camera

*Includes looking at models while foraging.

Table A2

Ethogram of behaviours for hopping mice visiting food trays indicating the behaviours included in each of the behavioural categories analysed

Behaviour	Description
Standing-looking	
Standing and looking (general)	Remaining still, head up, sharp turns of the head, listening. Includes elongated upright posture, using tail to balance. Investigatory and alert behaviour
Standing and looking (conspecific)	As above, but looking at conspecific
Standing and looking (model)	As above, but looking at model
Standing and sniffing (air)	Remaining still, head down or up sniffing with clear use of nose. Includes elongated upright posture, using tail to balance. Investigatory and alert behaviour
Moving quickly	
Moving quickly (general)	Fast-paced bipedal hop or ricochet. Mode of travel outside of cover
Moving quickly (finding cage entrance)	As above but navigating to cage entrance
Moving and foraging	Slow-paced bipedal walk or hop, while holding or ingesting food
Foraging	
Foraging-general	Remaining still in crouch position. Head up or down, ingesting food. Both hands used to hold food while ingesting. If it stopped eating to look around, it was considered standing-looking

Table A2 (continued)

Behaviour	Description
Foraging—facing model head on	As above, but facing model head on
Foraging—facing model side on	As above, but facing model side on
Foraging—back to model	As above, but back to model
Moving slowly	
Moving slowly	Slow-paced quadrupedal or bipedal walk or hop. Head is up and forward
Moving and sniffing	Slow-paced quadrupedal walk or hop. Head down with clear use of nose. Investigatory behaviour
Moving slowly (finding cage entrance)	As above but navigating to cage entrance
Visual	
Out of sight	Out of sight of camera

Table A3

Sample size of videos scored for behavioural analysis (after videos with animals on screen for less than 10 s were removed) for each experiment

Species	Experiment	Treatment	Stimuli	No. of videos	Popholes detected*		
Burrowing bettong	Body odour	Control	Control odour	14			
			Rabbit	14			
			Quoll	16			
			Cat	14			
			Control odour	10			
		Quoll-exposed	Rabbit	9			
			Quoll	11			
			Cat	7			
			Faeces	Control	Control sand	22	
					Rabbit	20	
	Quoll	18					
	Cat	20					
	Control sand	9					
	Model	Control	Rabbit	8			
			Quoll	13			
			Cat	9			
			Bucket	14			
			Rabbit	14			
		Quoll-exposed	Quoll	17			
			Cat	14			
Bucket			10				
Rabbit			9				
Quoll			11				
Spinifex hopping mice	Habitat	Control	Cat	7			
			Open	74	9/10		
			Cover	59	7/10		
		Quoll-exposed	Open	70	10/10		
			Cover	70	10/10		
			Cat-exposed	Open	66	9/10	
		Model	Control	Cover	48	8/10	
				Bucket	45	7/8	
				Rabbit	45	7/8	
	Quoll-exposed		Quoll	47	8/8		
			Cat	55	7/8		
			Bucket	49	8/8		
	Cat-exposed	Control	Rabbit	46	8/8		
			Quoll	33	8/8		
			Cat	56	8/8		
		Quoll-exposed	Bucket	29	7/8		
			Rabbit	33	8/8		
			Quoll	31	7/8		
Cat-exposed	Control	Cat	40	6/8			

*Popholes detected = number of active popholes with hopping mice detected on camera at food tray/number of active popholes attempted.

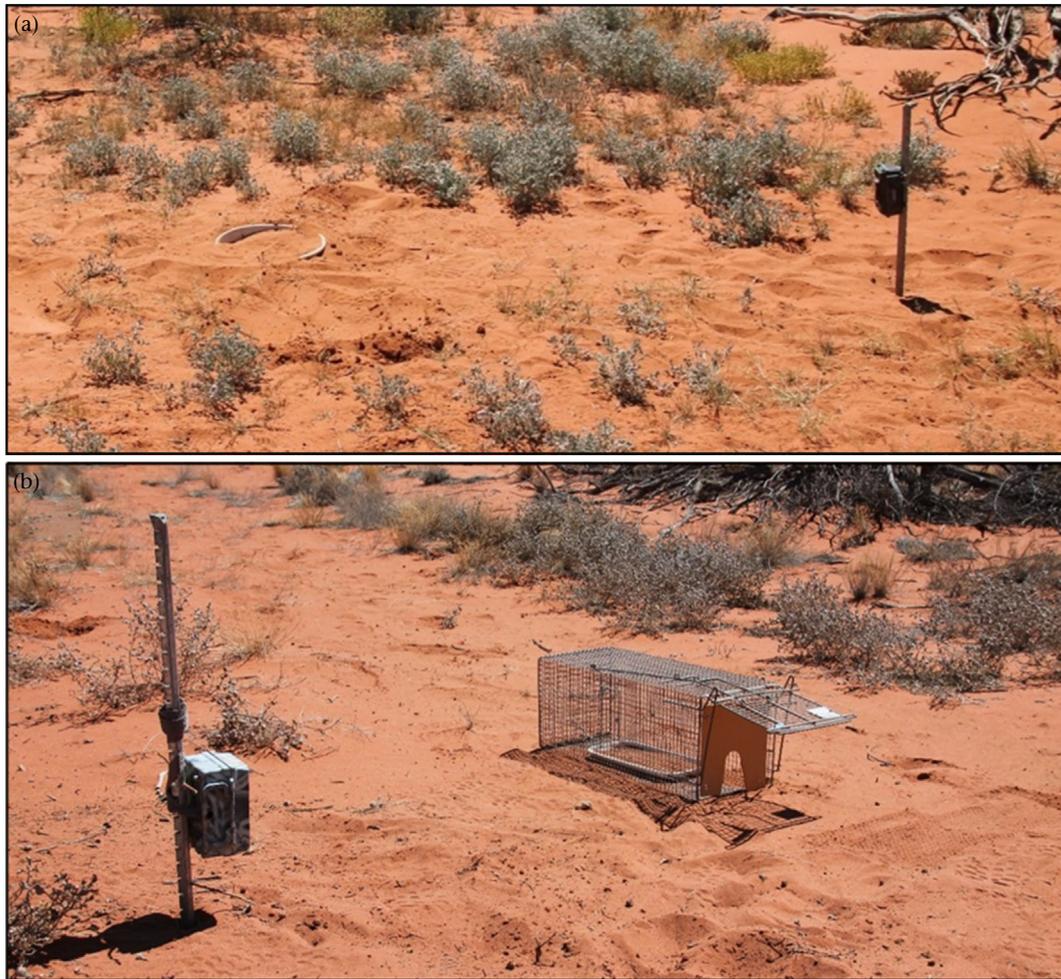


Figure A1. Set-up of camera trap set up at food tray for foraging experiments: (a) bettongs and (b) spinifex hopping mice. Stimuli not shown.

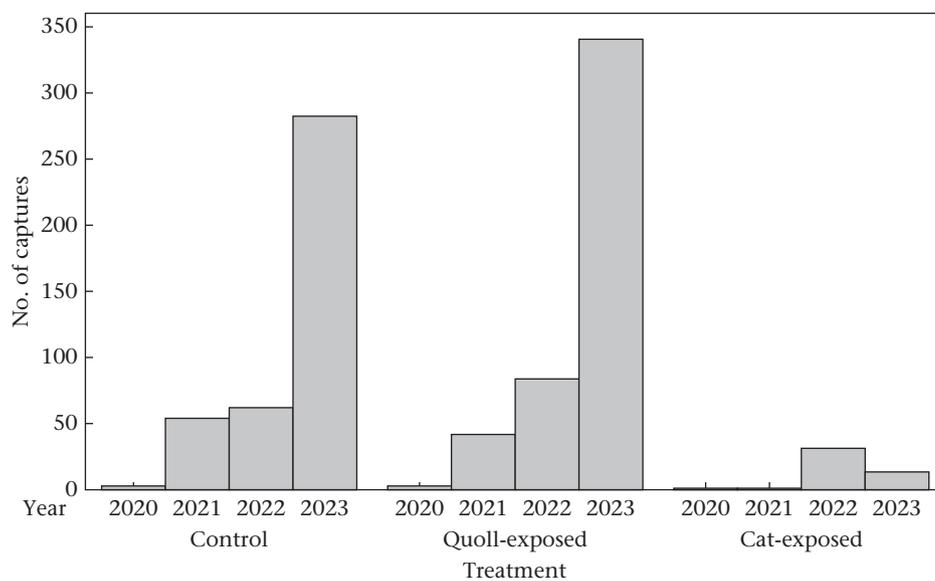


Figure A2. Total number of spinifex hopping mice captures per annual pitfall survey by treatment, conducted at Arid Recovery (see [Moseby et al., 2009](#) for methods). Data: Arid Recovery. Surveys in 2020 and 2022 were conducted in dune habitats and those in 2021 and 2023 in swale habitats. Sampling effort was the same for each annual survey.

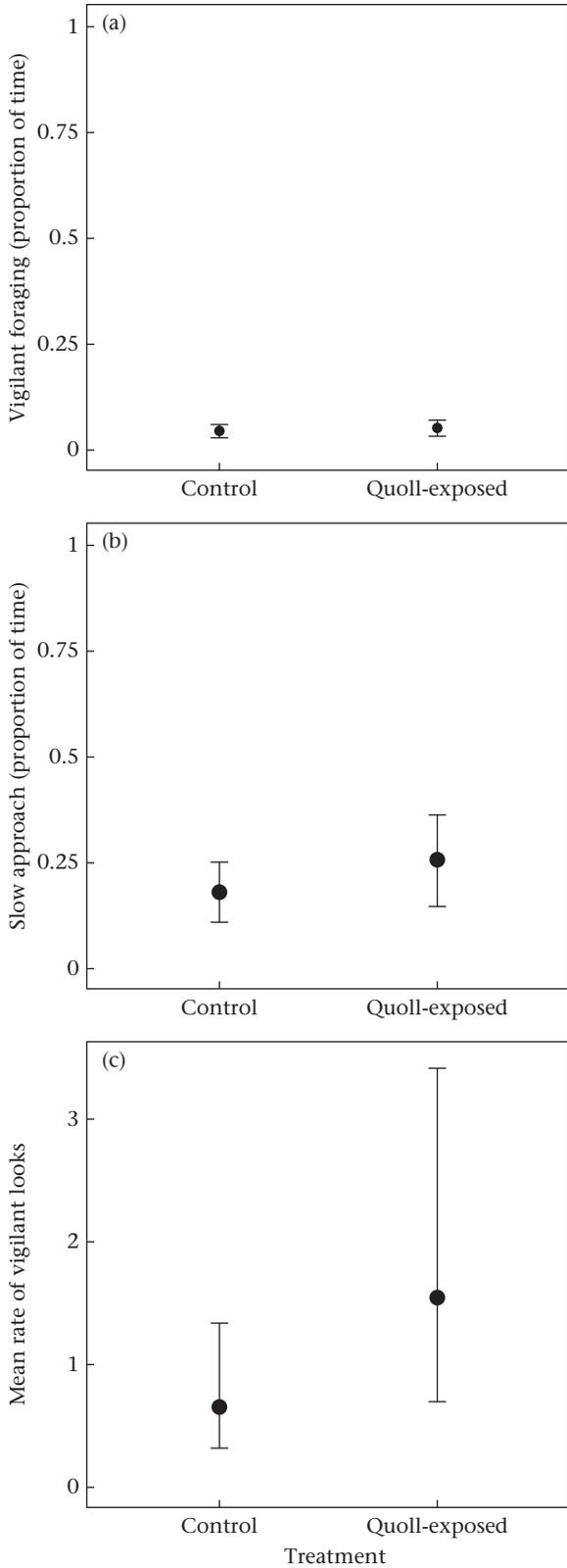


Figure A3. Predicted proportion of time spent by bettongs at foraging trays: (a) vigilant foraging behaviours (head up), (b) slow approach and (c) predicted rate of vigilant head looks while foraging (rate from time on screen). Control: $N = 27$; quoll-exposed: $N = 17$. Bars are 95% confidence intervals.

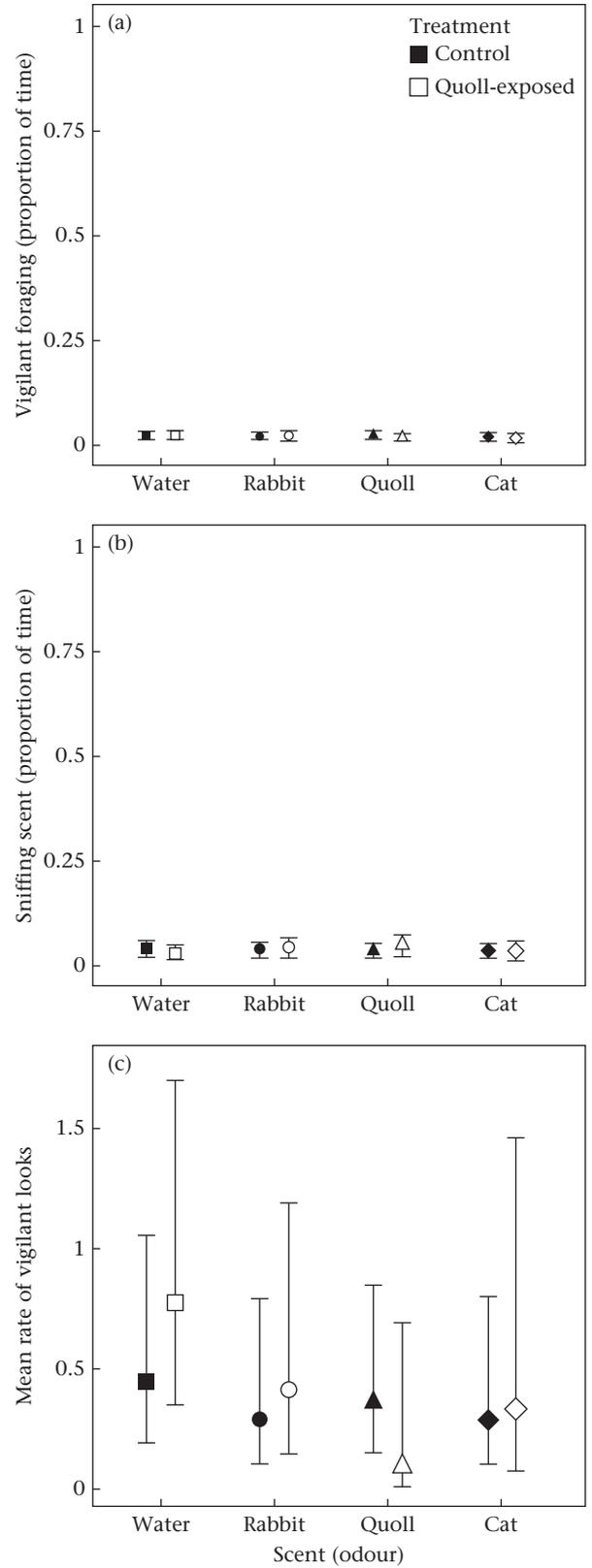


Figure A4. Predicted proportion of time spent by bettongs at foraging trays with different scented towels: (a) vigilant foraging behaviours (head up), (b) sniffing scented towels and (c) predicted rate of vigilant head looks while foraging (rate from time on screen). Control bettongs: control (water) $N = 14$; quoll scent: $N = 16$; cat scent: $N = 14$; rabbit scent: $N = 14$; quoll-exposed bettongs: control (water): $N = 10$; quoll scent: $N = 11$; cat scent: $N = 7$; rabbit scent: $N = 9$. Bars are 95% confidence intervals.

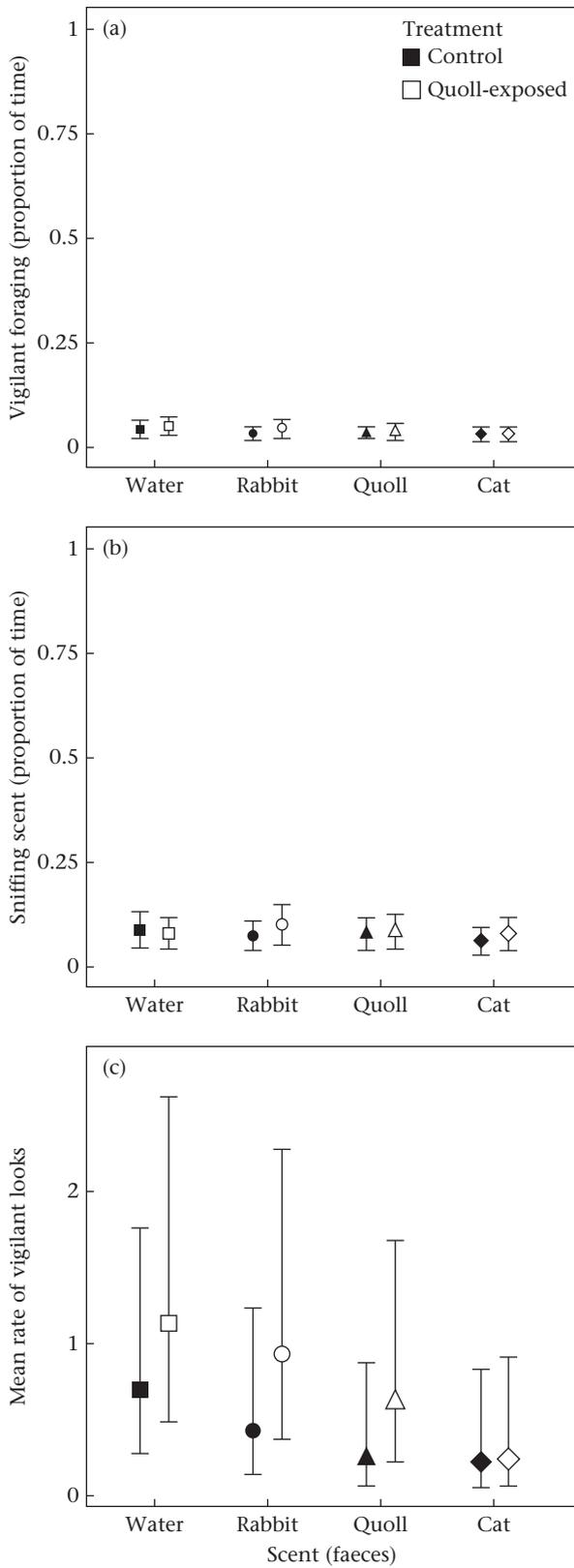


Figure A5. Predicted proportion of time spent by bettongs at foraging trays with different scented sand (scats): (a) vigilant foraging behaviours (head up), (b) sniffing scented sand and (c) predicted rate of vigilant head looks while foraging (rate from time on screen). Control bettongs: control (water): $N = 22$; quoll scent: $N = 19$; cat scent: $N = 20$; rabbit scent: $N = 20$; quoll-exposed bettongs: control (water): $N = 9$; quoll scent: $N = 13$; cat scent: $N = 9$; rabbit scent: $N = 8$. Bars are 95% confidence intervals.

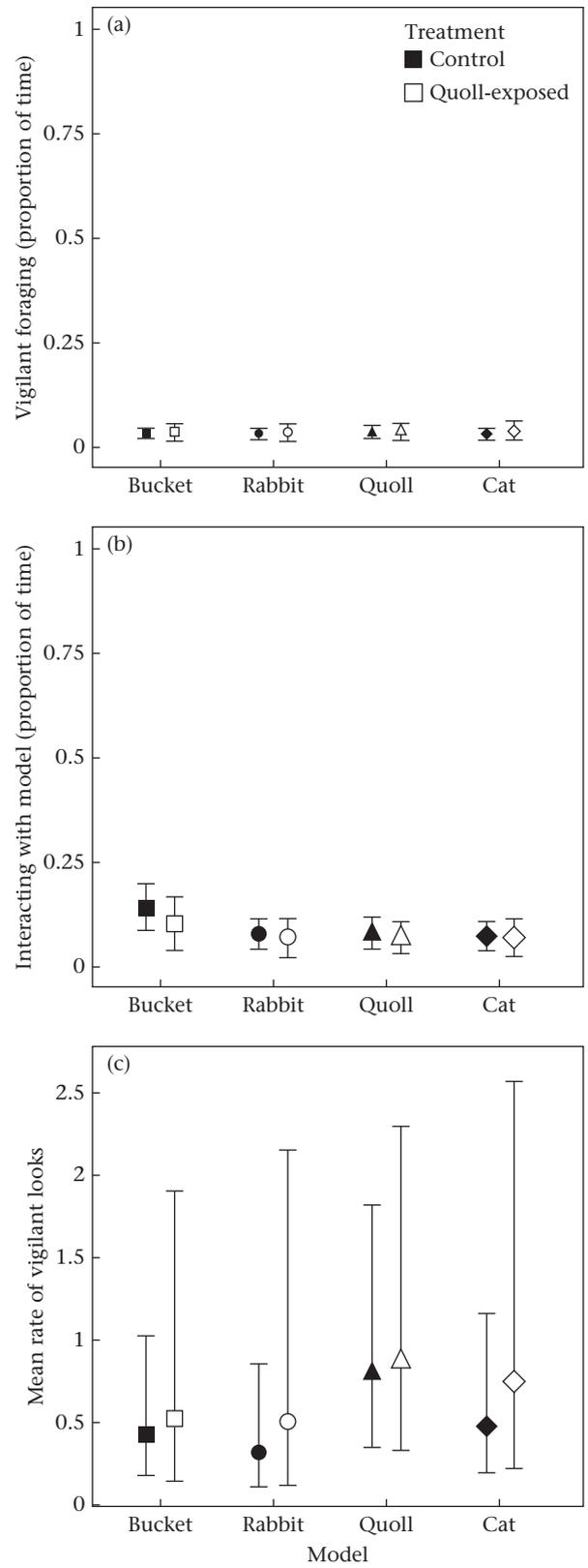


Figure A6. Predicted proportion of time spent by bettongs at foraging trays with different models: (a) vigilant foraging behaviours (head up), (b) looking at or interacting with model and (c) predicted rate of vigilant head looks while foraging (rate from time on screen). Control bettongs: control (bucket): $N = 14$; quoll model: $N = 16$; cat model: $N = 14$; rabbit model: $N = 14$; quoll-exposed bettongs: control (bucket): $N = 10$; quoll model: $N = 11$; cat model: $N = 7$; rabbit model: $N = 9$. Bars are 95% confidence intervals.

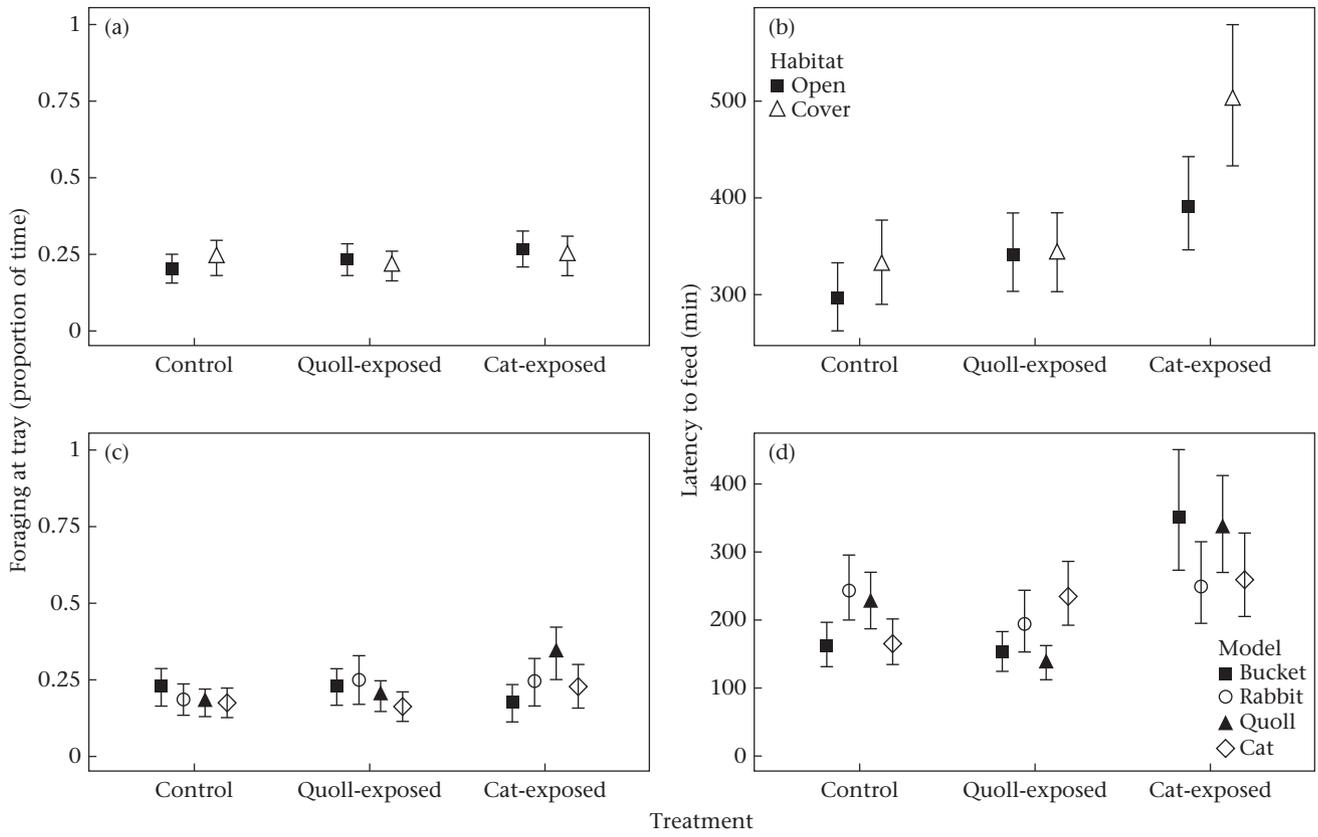


Figure A7. Responses of spinifex hopping mice at foraging trays. (a, b) Responses in open and covered habitats (133 control mice: 74 open, 59 cover; 140 quoll-exposed mice: 70 open, 70 cover; 114 cat-exposed mice: 66 open, 48 cover): (a) proportion of time spent foraging at tray and (b) latency to feed (min after sunset). Responses to different models (192 control mice: 45 bucket, 45 rabbit, 47 quoll, 55 cat; 184 quoll-exposed mice: 49 bucket, 46 rabbit, 33 quoll, 56 cat; 133 cat-exposed mice: 29 bucket, 33 rabbit, 31 quoll, 40 cat): (c) proportion of time spent foraging at tray and (d) latency to feed (min after sunset). Bars are 95% confidence intervals.