Behavioral
Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2023), 34(1), 63–75. https://doi.org/10.1093/beheco/arac097

Original Article

Can native predators be used as a stepping stone to reduce prey naivety to novel predators?

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Received 17 May 2022; revised 9 September 2022; editorial decision 21 September 2022; accepted 29 September 2022; Advance Access publication 11 November 2022

Predator naivety negatively affects reintroduction success, and this threat is exacerbated when prey encounters predators with which they have had no evolutionary experience. While methods have been developed to inculcate fear into such predator-naïve individuals, none have been uniformly successful. Exposing ontogenetically- and evolutionary-naïve individuals first to native predators may be an effective stepping stone to improved responses to evolutionarily novel predators. We focused on greater bilbies (*Macrotis lagotis*) and capitalized on a multi-year mammalian recovery experiment whereby western quolls (*Dasyurus geoffroii*) were reintroduced into parts of a large fenced reserve that contained a population of naïve bilbies. We quantified a suite of anti-predator behaviors and measures of general wariness across quoll-exposed and quoll-naive bilby populations. We then translocated both quoll-exposed and quoll-naïve individuals into a large enclosure that contained feral cats (*Felis catus*) and monitored several behaviors. We found that bilbies can respond appropriately to quolls but found only limited support that experience with quolls better-prepared bilbies to respond to cats. Both populations of bilbies rapidly modified their behavior in a similar manner after their reintroduction to a novel environment. These results may have emerged due to insufficient prior exposure to quolls, inappropriate behavioral tests, or insufficient predation risk during cat exposure. Alternatively, quolls and cats are only distantly related and may not share sufficient similarities in their predatory cues or behavior to support such a learning transfer. Testing this stepping stone hypothesis with more closely related predator species and under higher predation risk would be informative.

Key words: **anti-predator trait, greater bilby, marsupial, neophobia, predator–prey.**

INTRODUCTION

Introduced predators have a disproportionately greater impact on prey than native predators (Salo et al. 2007), in part due to prey naivety (Carthey and Blumstein 2018). The absence of co-evolution in novel predator–prey interactions has led to catastrophic declines, particularly on islands where the introduction of invasive predators has decimated populations of native vertebrates (Fritts and Rodda 1998; Dowding and Murphy 2001; Woinarski et al. 2015; Russell and Stanley 2018). Naivety can include failure to recognize predators as a threat or the engagement of inappropriate anti-predator responses (Banks et al. 2018). Prey naivety is considered to be ontogenetic or evolutionary depending on whether the animal has been isolated from a predator during its lifetime or over evolutionary time scales, respectively (Carthey and Blumstein 2018). Evolutionary naivety is considered more difficult to address because animals have to evolve novel responses to these predators with which they have had no prior experience (Griffin et al. 2000).

Designing appropriate methods to reverse prey naivety is essential for conservation species threatened by predation from novel predators. Some studies have used classical conditioning to train captive prey to respond to predator cues (Griffin et al. 2000). Recently, direct exposure (or in situ training) to low-level predator densities in the wild has been proposed as a more realistic way to address prey naivety (Moseby et al. 2016; West et al. 2018). This context provides prey species with opportunities to learn or adapt

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their behavior through direct exposure to wild predators, which eliminates the need to use simulated predator cues (Moseby et al. 2015, 2016; Blumstein et al. 2019). Using live predators and exposing prey under wild conditions may provide more realistic and holistic predator cues (Griffin et al. 2000) and stimulate learning and adaptation without the need for managers to create classical conditioning opportunities. Prerelease exposure of native species to feral cats has shown improved survival in greater bilbies (Ross et al. 2019) and the development of enhanced vigilance and reactivity in burrowing bettongs (*Bettongia lesueur*) compared with control populations (Saxon-Mills et al. 2018; West et al. 2018; Tay et al. 2021).

While initial results of prerelease exposure are promising, addressing evolutionary naivety may benefit from a more staged approach to predator exposure. For example, exposure of ontogenetic and evolutionary naïve prey first to native predators may provide a necessary stepping stone to overcome evolutionary naivety to novel predators. The reasons for this are 2-fold. First, the multi-predator hypothesis suggests that exposure to one predator species should improve the behavioral responses to another predator species (Blumstein 2006), and this response may be enhanced if the predators share similar archetypes (Cox and Lima 2006). Second, prey responses should develop faster from exposure to native rather than introduced predators because they have a shared evolutionary history (Cox and Lima 2006).

The greater bilby (*Macrotis lagotis*) is a threatened marsupial whose range has declined by over 70% since the European settlement of Australia. Bilbies have co-existed with native predators such as the western quoll (*Dasyurus geoffroii*) for millions of years, with dingoes (*Canis lupus dingo*) for thousands of years, and with introduced predators, such as the feral cat (*Felis catus*) and red fox (*Vulpes vulpes*) for only 200 years. A recent meta-analysis highlighted that many Australian native species can recognize threats posed by invasive predators like foxes and cats, despite little or no historical contact with these species (Banks et al. 2018). This may be due to these species possessing predator archetypes similar to the native predators found in Australia (Cox and Lima 2006). Bilbies have been shown to respond to predator scents under free-living and predator-free conditions. For example, bilbies in predator-free environments appeared to distinguish between canid feces compared with feline, rabbit, and control scents and showed more vigilant responses (Steindler et al. 2018). Similarly, in wild populations, bilbies appeared to spend more time investigating (sniffing) canid and feline scents compared with non-predatory scents (Steindler and Letnic 2021). These results suggest that bilbies have retained some level of predator recognition that may be scaled with the period of co-evolution to different predators. Attempts to improve the bilbies' response to feral cats using in situ predator training in the wild with live cats have shown promise; a study comparing bilbies from predator-free and cat-exposed populations showed improved anti-predator behavior and survival after release in cat-exposed bilbies (Ross et al. 2019).

We sought to determine if exposing greater bilbies to wild quolls (a historically important predator) could act as a "stepping stone," and improve bilbies' anti-predator responses to cats (an evolutionary and ontogenetically novel predator) under wild field conditions. Previous studies have found other prey species to adjust their behavior when exposed to quolls (Jolly et al. 2021), so we predicted that quoll-exposed bilbies would also show behavioral shifts. To test this, we conducted four experiments to investigate behavioral and spatial responses to different cues most likely to elicit an anti-predator response. In Experiment 1, we investigated whether bilbies exposed to native predators responded with more vigilant behavior to predator models than quoll-naive bilbies, as visual recognition is an important mechanism that many species use to detect predators. In Experiment 2, we asked whether bilbies exposed to quolls modified their vigilance and wariness in response to live native predator cues. In Experiment 3, we tested whether bilbies exposed to native quolls responded with a higher level of wariness and increased cover choice when placed in novel environments. Finally, in Experiment 4, we asked if native quoll-exposure transferred over to improved anti-predator behavior toward cats. We hypothesized that bilbies exposed to quolls would increase their wariness and vigilance compared with quoll-naive populations and have better survival. We predicted that this improvement would also enhance anti-predator traits to cats in the quoll-exposed group. Ultimately, we comprehensively interrogated bilby anti-predator behavior to better understand whether exposure to quolls modified bilby behavior in such a way that may ultimately enhance survival in the presence of novel predators.

METHODS

Study area

Bilby experiments were conducted at the Arid Recovery Reserve in northern South Australia. The climate is arid and rainfall is low and erratic, averaging 168 mm annually (Read 1995). Habitat in the reserve includes *Acacia* sand dunes, sandplains, ephemeral swamps, and chenopod shrubland swale habitats (Moseby and O'Donnell 2003). Arid Recovery is a fenced reserve with six paddock-sized areas portioned into fenced exclosures designed to limit the movement of some species (Moseby and Read 2006; Moseby et al. 2018). Species reintroduced to the area include greater bilbies in 2000, burrowing bettongs in 2001, Shark Bay bandicoots (*Perameles bougainville*) in 2001, and western quolls in 2015. One paddock (1400 ha) is maintained as a predator-free control paddock where an additional electric fence restricts access by both native quolls and introduced predators. Three other adjoining paddocks form the quoll paddock (4600 ha) where the western quoll has been reintroduced and co-exists with the reintroduced native prey species, including the bilby (Figure 1a). Introduced predators are not present in either the control or quoll paddock. Although quolls have been reported to breach the control paddock (West et al. 2020), additional netting has since been added to reduce this likelihood, and regular surveillance along with immediate capture and removal of incursions is now undertaken (Arid Recovery, unpublished data). Regular long-term track counts in each paddock (transect range 2.2 - 7.9km) have shown track counts to be extremely low (mean < 0.24/km) and intermittent (18.2% of transects) in the control paddock, and low but persistent in the quoll paddocks (mean 3.75/km, 91.3% of transects; Arid Recovery, unpublished data). Furthermore, quoll density had likely reached carrying capacity in the quoll paddocks as monitoring found many sub-adult individuals dispersed over the fence and left the reserve and was having significant impacts on other prey species within the reserve (Arid Recovery, unpublished data). Consequently, we feel that the control paddock represented an adequate control group that allowed for testing behaviors between the two populations. At the time of the experiment, bilbies had been co-existing with quolls in the quoll paddock for at least 5 years.

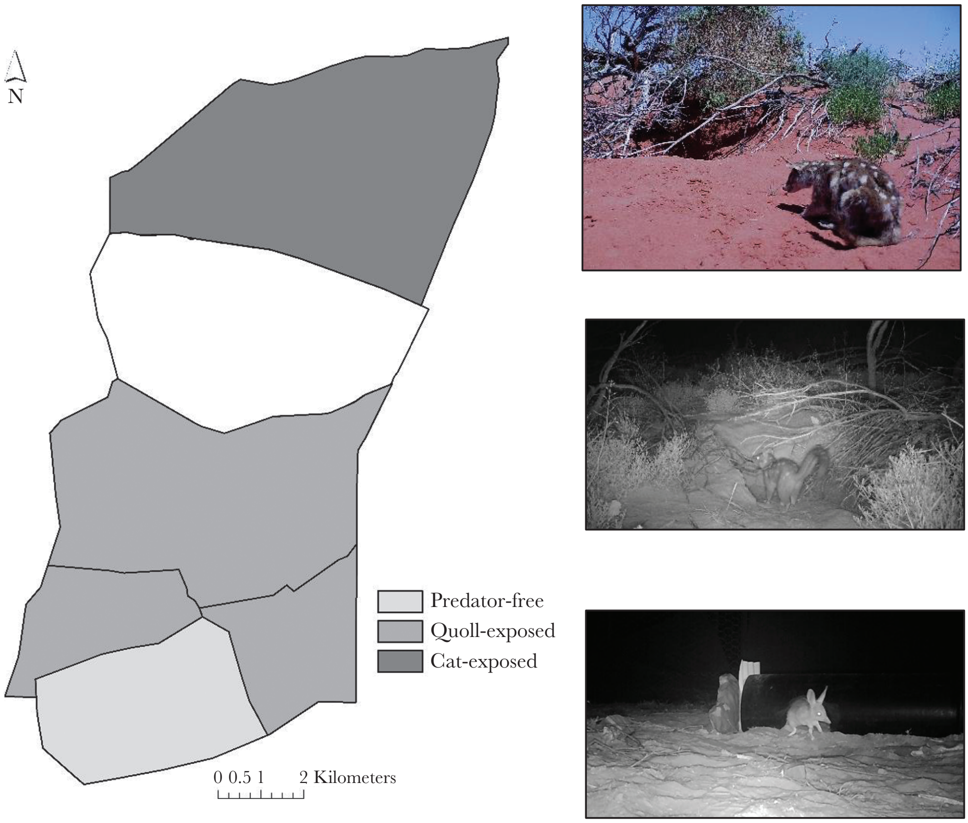

Figure 1
Images showing: (a) Paddocks within Arid Recovery, (b) placement of a quoll model outside a bilby burrow from Experiment 1, (c) presence of a live quoll at a burrow used by bilbies from Experiment 2, and (d) bilby emerging from the artificial burrow in the novel pen from Experiment 3.

Bilbies were initially captured at night from the control and quoll paddocks during September and November 2020 using spotlights and handheld fishing nets (Moseby et al. 2012). Bilbies were weighed, measured, and 9 g core tail mount Very High Frequency transmitters (Lotek) were attached to individuals greater than 650 g as described in Moseby et al. (2012). A second group of bilbies were captured from both control and quoll paddocks in June 2021 and relocated to a novel environment (a large paddock) with a novel predator (feral cat) and their movement and survival were monitored for up to three months after release (see below for details).

Experiment 1: Response to predator models

To test the hypothesis that exposure to quolls modified the ability of bilbies to visually recognize predators, we exposed bilbies with different histories of predator exposure to taxidermy models of rabbits, quolls, and cats, and a procedural control (a plastic bucket) within their relevant paddock (Figure 1b). We expected that bilbies from the quoll paddocks would be more likely to show anti-predator responses to quolls and possibly cats compared with quoll-naive bilbies. Bilbies with tail transmitters were tracked to a burrow during the day when they are inactive, and a single model was placed approximately 1–2 m from the burrow entrance. Two motion-activated camera traps (Swift Enduro, Outdoor Cameras Australia) were placed at 90° angles to obtain photographic and video footage of bilbies' responses to the models immediately after burrow emergence or immediately before entering a burrow. Cameras were set to record two photos and a 60 s video after detection any time between dusk and dawn, which is the period of bilby surface activity. Despite two cameras being placed at each bilby burrow when models were present, we were unable to capture behavioral videos of bilbies from every burrow for every model, because some individuals did not leave the burrow or possibly left from a different exit. We aimed to rotate models over consecutive nights at a given bilby burrow after a Latin square design to ensure the order of presentation did not affect potential responses. However, in some cases, if a bilby could not be located the following day, we continued the experiment once the bilby had been found but still following the original Latin square order. We also recorded if bilbies moved to a different burrow or not, after each model presentation, and recorded the distance moved between burrows relative to each model type.

For each model, we used the first video response that was ≥5 s long to capture the initial response of bilbies. We used videos from bilbies with and without tail transmitters to increase the sample size. We used the event logging software BORIS v. 7.9.22 (Friard and Gamba 2016) to score the proportion of time when visible that bilbies were engaged in specific behaviors following an ethogram (Supplementary Information SI 1). When bilbies were visible, we recorded the time spent moving (stationary, slow, fast), sniffing (air, ground, model), bipedal stance, foraging, digging, or looking at a model. We also noted whether bilbies were near (<0.5 m) or far (>0.5 m) from the model. All videos were scored blind concerning the treatment group and location and conducted by the same observer. Because some behaviors were difficult to distinguish separately, we pooled some behaviors into categories (see Supplementary Information SI 1), leading to four categories for final analysis: time near model, time looking at models, time spent stationary, and time engaged in investigative behaviors. We did not have enough data to compare bipedal, digging, or foraging behavior.

Experiment 2: Natural responses to a live predator

To investigate how prior predator exposure influenced the responses of bilbies to real predators, we recorded how bilbies responded to visits to their burrow entrances by quolls. To provide a reference condition, we included the behavior of bilbies in the control paddock that had not been exposed to quolls and divided the bilbies in the quoll paddock into those with and without recent visits to burrow entrances by live quolls. We expected that bilby behavior would show increased wariness following a recent visit by quolls, compared with periods when quolls were not present or to quoll-naive bilbies. We placed a camera 3–4 m from the burrow entrance at a total of 47 actively used bilby burrows. Cameras were set to record two photos and a 60 s video in both the summer and winter periods from dusk to dawn. All visits by native quolls to a burrow entrance (Figure 1c) were noted along with the time until the next bilby video (max. 24 h).

We filtered videos to use only the first video of a bilby per location per day. Behaviors recorded included the presence of bilbies close (<1 m) or far (>1 m) from the burrow entrance. We used a similar ethogram to Experiment 1, but modified some behaviors that were not relevant to responses to models (Supplementary Information SI 1). When bilbies were visible, we recorded the time spent moving (stationary, slow, fast), sniffing (air or ground), bipedal stance, foraging, or digging. Videos were categorized into two different periods, either evening (before midnight) or dawn (midnight to dawn), to account for potential differences related to the time of night. We divided the videos into three treatment groups, bilbies from the control paddock (Quoll-naive), bilbies from the quoll paddock but no quoll presence in the previous 24 h (Quoll-no recent visit), and bilbies from the quoll paddock with quoll presence (Quoll-recent quoll visit). All videos were scored blind concerning the group, location, or period of data collection by the same observer. We did not have enough data to compare moving fast, bipedal, digging, or foraging behavior.

Experiment 3: Novel environment (small pen, predators absent)

To test the hypothesis that prior predator exposure would influence bilby responses in novel environments, we placed bilbies from quoll-naive and quoll-exposed populations into a novel, predator-free environment and measured their behavioral responses. We expected that quoll-exposed bilbies would have higher vigilance compared with quoll-naive bilbies. On the evening following capture, bilbies from both control and quoll paddocks were placed individually in a small fenced enclosure after dark and filmed using a handheld night vision camera (Bushnell Equinox 72) from a hide. Three-quarters of the pen was bare ground, with one-quarter of the area having low vegetation cover to mimic similar habitat in the reserve. An artificial burrow was placed in the center and the exit hole was covered (Figure 1d). The cover could be removed from outside the pen by the observer without being seen by the bilby. Bilbies were placed in the burrow, allowed to settle briefly, and then the exit covering was removed when the observer left the pen and entered the hide, as per Ross et al. (2019). We recorded the latency to exit the artificial burrow and then filmed bilbies after emergence for approximately 10 min, before recapturing them and releasing them at the original site of capture. We quantified, from the video and using BORIS, the proportion of time spent engaged in several behaviors that were pooled into several categories (Supplementary Information SI 1) due to limited sample size in some cases: stationary, moving fast, sniffing, and agitated. We did not analyze digging or foraging behavior due to small sample sizes. Additionally, we scored the proportion of time spent in each of the habitats (open, vegetated). Wind (mild or strong) was recorded as another potential fixed effect. All videos were scored blind with no knowledge of the bilby population, sex, or period caught.

Experiment 4: Novel environment (large paddock, novel predators present)

Finally, we investigated whether bilbies exposed to native predators would have improved vigilance behavior compared with quoll-naive bilbies when exposed to novel predators (cat). We translocated bilbies from both groups into a large paddock with feral cats and monitored their burrow use and movement after release. We expected bilbies with prior predator exposure to select burrows and respond spatially in ways that would reduce predation risk. In June 2021, a random selection of 30 bilbies (15 control paddock and 15 quoll paddock) were captured and moved to a large novel environment (cat paddock 3700 ha) containing an estimated 10 feral cats. These bilbies were radio-tracked for up to three months post-release and survival, burrow location, and movements were recorded. In some cases, an individual was not found after release, or transmitters fell off. Where possible, bilbies were re-trapped and the transmitter reattached during the study. We measured the distance moved between burrows used on consecutive days per bilby and removed any days immediately after trapping, as trapping may have influenced the movement. We compared burrow use of quoll-exposed and quoll-naive bilbies before (quoll-exposed source, quoll-naive source) and after (quoll-exposed translocated, quoll-naive translocated) release into the cat paddock. Data were collected from different radio-tracked bilbies in the control and quoll paddocks (between September 2020 and March 2021) due to logistical difficulties in following the same individuals. We recorded burrow location and burrow characteristics (habitat—top dune, side dune, edge dune, sandplain, swale; the number of functional entrances and average burrow entrance exposure—open, partially covered, or covered by vegetation). Because of the limited sample size in some habitats, we pooled top dune, side dune, and edge dune into a single dune category and sandplain and swale areas as a non-dune category.

Data analysis

For Experiment 1, we compared whether bilbies from quoll-exposed and quoll-naive populations moved burrows or remained at the same burrow in response to a particular model using a generalized linear mixed model (GLMM) with a binomial distribution. We also compared the distance moved between burrows after model presentation using a zero-inflated linear model with a gamma (log link) distribution. In both cases, we included bilby sex and order of model placement as additional fixed effects and bilby identity as a random effect. However, if not significant, these variables were removed to simplify models, but we retained interactions as this was our primary hypothesis for testing. For our video data, we pooled some behaviors into similar categories due to low sample size (Supplementary Information SI 1) and used these as our response variables. The time allocated to each specific behavior was calculated as a proportion of the total visible time (W) for each video. Since these response variables were proportions resulting from continuous measurements, we used beta regression distributions with a logit link for our analyses and included precision variables (φ) with an identity link to capture potential variation in covariates to improve estimates of model parameters (Ferrari and Cribari-Neto 2004; Douma et al. 2019). In some cases, a specific behavior was not observed on video for an individual bilby, leading to zeros in our data. Because beta distributions require observations between zero and one, we rescaled our data in these cases after the equation described in Douma et al. (2019). For behavioral comparisons, we used population source (quoll-naive and quoll-exposed), model treatment, and a population by model interaction term as fixed effects. We included time visible in the video, population, model order, and burrow location as precision terms. Where precision variables were not significant, we tested the importance of retaining these variables in the model using likelihood ratio tests (LRT).

For Experiment 2, we followed similar analyses as above when comparing three behavioral categories from our model experiment video data (Supplementary Information SI 1). However, in this case, our fixed effect was the treatment group (quoll-naive, no quoll at burrow entrance, quoll present at burrow entrance) and video period. We included time visible, video period, and population source as precision terms. Precision terms were removed from the model if they were not significant as described above.

For Experiment 3, we analyzed video behavior as described in Experiment 1. We used population source and sex as our fixed effects and tested interactions between these. We also checked whether wind speed also influenced behavior. We used time visible and population source as precision terms. However, we removed wind speed, precision terms, and interactions to simplify models if they were not significant. For latency to emerge, we log-transformed the response variable to meet model assumptions.

In Experiment 4, we used treatment group (quoll-naive source, quoll-naive translocated, quoll-exposed source, quoll-exposed translocated) and sex as fixed effects in each of our three burrow attribute analyses. We included bilby identity as a random effect. To compare the number of functional entrances, we used a GLMM with a zero-truncated negative binomial distribution. For burrow habitat, the proportions of each habitat used overall differed greatly; therefore, we pooled habitats as either dune (top, side, edge), and not dune (sandplain, swale) and used a GLMM with a binomial distribution to compare the probability of bilbies selecting burrows in these two habitats. Finally, to compare differences in burrow entrance exposure, we used ordinal logistic regression with a random effect of bilby ID because exposure ranged from open to increasing cover. We compared daily distance traveled between burrows, using population and sex as fixed effects and bilby ID as a random effect. We fitted a linear mixed model with a zero-inflated gamma distribution with a log link, due to a large number of zeros in the data when bilbies did not move burrows.

All analyses were conducted in R v.4.0.1 (R Core Team 2020) using the packages betareg (Ferrari and Cribari-Neto 2004), lmtest (Zeileis and Hothorn 2002), glmmTMB (Brooks et al. 2017), ordinal (Christensen 2019), and move (Kranstauber et al. 2020). Where the same bilby or burrow was used under repeated settings, we included bilby ID or burrow ID as a random effect in the relevant analyses and tested the importance of these variables using LRT. We checked our model fit visually by plotting residuals (using sweighted2 residuals for beta regression models) and testing for overdispersion in the package DHARMa (Hartig 2020). We also looked for influential outliers using residual plots and where considered removal of these points, we analyzed data with and without them and report results of both analyses. Where relevant, we used bootstrapping with 1000 simulations to estimate 95% confidence intervals for models containing random effects to improve the accuracy of beta coefficients using the package parameters (Ludecke et al. 2020) and these are shown in brackets. All plots show predicted estimated marginal means from the package emmeans (Lenth 2020) and plotted using ggplot2 (Wickham 2016). We also calculated a standardized effect size using the package emmeans for models where population was a fixed effect to look at the strength of any population differences.

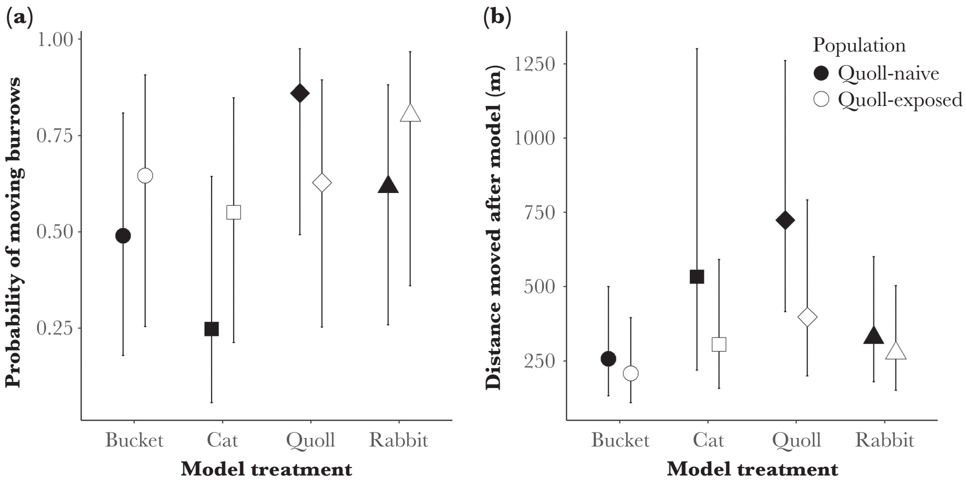

Figure 2

Model experiment results between quoll-naïve and quoll-exposed bilbies showing (a) probability of moving burrows in response to a particular model, and (b) the mean distance moved after placement of a model. Results are averaged over sex and order (as relevant) with error bars showing 95% confidence intervals.

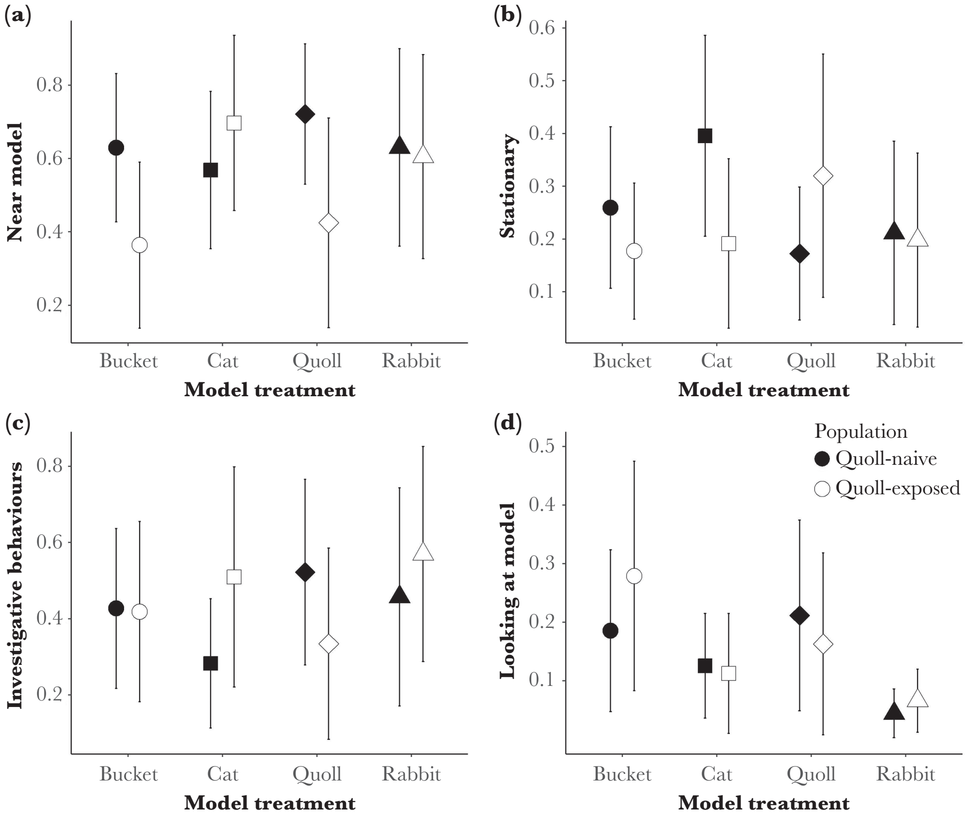

Figure 3

Predicted proportion of time spent by bilbies from quoll-naive and quoll-exposed populations in four behavioral categories: (a) near model, (b) looking at model (c) investigative behaviors, and (d) stationary, recorded at burrows with different model placements. Error bars show 95% confidence intervals.

RESULTS

Experiment 1: Response to model predators

We recorded movements from 21 bilbies following the presentation of visual stimuli (86% received the full model set), providing a total of 72 (quoll-naive = 38, quoll-exposed = 34) movement and distance data points. When considering whether bilbies moved burrows after exposure to a model, there were no interaction effects between model treatment and population (Figure 2a), suggesting predator exposure did not influence whether bilbies moved after model placement regardless of the model type. However, within the quoll-naive population, bilbies moved burrows significantly more often when presented with a quoll model compared with a cat model ($\beta = 2.92$, $z = 2.27$, $P = 0.023$). Male bilbies were 3.8 times more likely to move than females ($\beta = 1.34$, $z = 2.20$, $P = 0.028$). The order of models was important, with bilbies significantly less likely to move after the third model placement compared with the first model ($\beta = -2.00$, $z = -2.39$, $P = 0.017$) and to a lesser extent the fourth model ($\beta = -1.46$, $z = -1.78$, $P = 0.076$). We then compared the distance moved between burrows by bilbies after the placement of each model. We found a significant difference between the bucket and quoll model for the quoll-naive population, with bilbies moving further in response to the quoll model ($\beta = 1.04$, $z = 2.33$, $P = 0.02$). However, we found no other model differences, effect of model order, or significant interaction effects (Figure 2b). Mean distance, however, was also affected by sex with males moving on average larger distances than females overall ($\beta = 0.83$, $t = 3.02$, $P = 0.003$).

We extracted 52 behavioral videos at burrow entrances from both source populations (quoll-naive = 30, quoll-exposed = 22), with a minimum of five videos at independent burrows per model for each population. We used all available videos for analyses with mean visibility of bilby time of 27.1 s (standard deviation [SD] 19.1).

Results from the video analysis indicated that the quoll-exposed population spent more time close to and engaged in investigative behaviors in the presence of the cat and rabbit models, whereas the quoll-naive population showed more interest in the quoll model, although these differences were subtle (Figure 3). Specifically, bilbies from the quoll-exposed population spent more time near the cat model compared with the bucket ($\beta = 0.33$, z.ratio = 1.96, $P = 0.049$). There was a trend for quoll-exposed bilbies to spend less time at the bucket ($\beta = -0.27$, z.ratio = −1.70, $P = 0.089$) and the quoll model ($\beta = -0.30$, z.ratio = −1.68, $P = 0.093$), but neither of these reached significance (Figure 3a). We found a subtle interaction effect between the populations and the cat and quoll models although it did not reach significance ($\beta = 0.35$, z.ratio = 1.94, $P = 0.053$) for the time spent stationary. There was a tendency for quoll-naive bilbies to spend more time stationary at the cat model, whereas the quoll-exposed population was stationary longer in the presence of the quoll model (Figure 3b). Time spent looking at models or investigating models was not explained by any fixed or interaction effects. However, for investigative behaviors, both groups showed similar reactions to the bucket but differing responses to the other models (Figure 3c).

Experiment 2: Response to live predator

A total of 108 videos were extracted from all the camera traps placed outside burrows. However, we removed videos that had <10 s of video, leaving a total of 70 videos for analysis from 36 burrows (quoll-naive = 14, quoll-exposed—no recent visit = 18, quoll-exposed—recent quoll visit = 10). In general, there were indications that quoll-exposed bilbies were more active around their burrows after a recent quoll visit. One video, in particular, was found to highly influence the results with the bilby spending 62% of its time stationary, seven times larger than the mean of the bilbies from this group. Leaving in this outlier, we found no differences between the groups. However, when removing this outlier, bilbies from the quoll-exposed population whose burrows had recently been visited by a quoll spent less time being stationary around the burrow compared with both quoll-naive bilbies ($\beta = -1.48$, $z = -3.21$, $P < 0.01$) and bilbies not recently visited by a quoll ($\beta = -1.52$, $z = -3.323$, $P < 0.001$) (Figure 4b). For sniffing behaviors, there was no significant difference between the three treatment groups, although there was a slight trend toward increased sniffing time by the quoll-exposed group when quolls had visited recently. Similarly, we found no difference between the three treatment groups in the proportion of time bilbies spent near the burrow entrance.

Experiment 3: Novel environment (small pen, predator absent)

A total of 32 bilbies (13 quoll-naive: 7F 6M, 19 quoll-exposed: 6F 13M) were captured and placed in a novel small pen to record behavioral responses. The mean period of visibility was 464.4 s (SD = 75.25) for all bilbies. Bilbies from the quoll-exposed population (mean = 129.58 s) and quoll-naive population (mean = 85.79 s) did not differ in their time to emerge from the artificial burrow ($\beta = -0.201$, $t = -0.418$, $P = 0.679$) and there was no difference between the sexes ($\beta = 0.337$, $t = 0.731$, $P = 0.472$; Figure 5a). Five bilbies (4 quoll-naive, 1 quoll-exposed) managed to escape the burrow before the observer opened the entrance and were not included in this analysis.

A significant interaction was found for time spent in covered areas between population and sex ($\beta = -1.36$, $z = -2.71$, $P = 0.007$; Figure 5b). Females from the quoll-exposed population spent more time in covered areas than those from the quoll-naive treatment ($\beta = 0.18$, z ratio = 2.11 $P = 0.035$), whereas male quoll-exposed bilbies spent more time in the open than male quoll-naive bilbies ($\beta = -0.143$, z ratio = −1.79, $P = 0.074$). When comparing agitated behaviors, we found one influential outlier affecting results. When removing the outlier bilbies from the quoll paddock also spent more time agitated and trying to escape from the pen (see Supplementary Information SI 1) than quoll-naive bilbies ($\beta = 0.21$, $z = 2.18$, $P = 0.029$), with males also engaged in more agitated behaviors than females ($\beta = 0.21$, $z = 2.12$, $P = 0.034$; Figure 5d). Bilbies also spent more time engaged in agitated behaviors on less windy nights ($\beta = -0.28$, $z = -3.28$, $P = 0.001$). However, when we retained this data point, we found no differences for population or sex. Investigating further, we found this individual (quoll-exposed) spent much less time in agitated behaviors than other bilbies, as it remained in the one spot for more than half the time (291 s) while visible, which was >11 times longer than the mean of the remaining bilbies. Source population or sex were not significant predictors for the time spent sniffing areas away from the fence (Figure 5c). In this case, we also detected one outlier, but removing this observation did not change the overall results, so it was retained. We found no significant predictors for moving fast or stationary behavior.

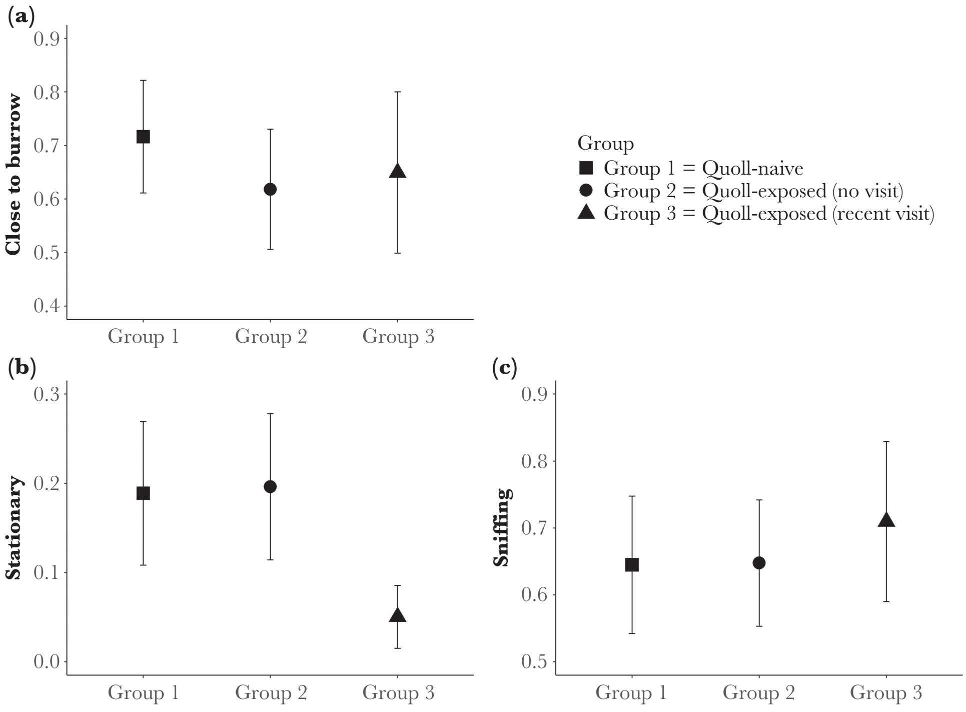

Figure 4
Predicted proportion of time spent by bilbies: (a) close to burrow, (b) stationary, and (c) sniffing, from a predator-free paddock (quoll-naive) and quoll-exposed paddock with and without a recent (<24 h) quoll visit to the burrow. Error bars show 95% confidence intervals.

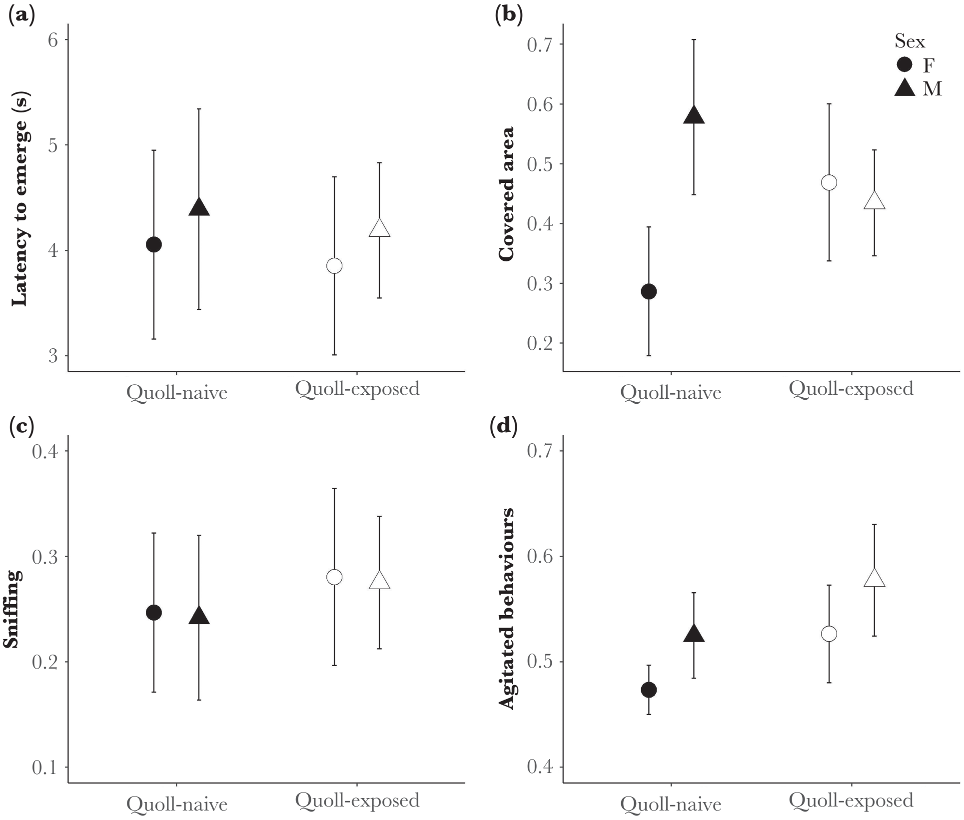

Figure 5
Behaviors exhibited by bilbies from quoll-naive and quoll-exposed populations when placed in a small novel experimental pen. Behaviors recorded were: (a) latency to emerge from burrow, (b) proportion of time spent in covered areas, (c) proportion of time moving slowly and sniffing, and (d) proportion of time in agitated and escape behaviors. Error bars represent 95% confidence intervals.

Experiment 4: Novel environment (large paddock, novel predator present)

We collected data on burrow characteristics from 664 burrows used by 55 (21F 34M) bilbies across control and quoll-exposed paddocks both before and after being moved to the cat paddock (mean 12 burrows per individual, range: 1–30). We compared four independent treatment groups (quoll-naive source = 55, quoll-naïve translocated = 267, quoll-exposed source = 123, quoll-exposed translocated = 219). Sex was not a significant predictor in any model and was removed from the analysis. First, we compared the number of burrow entrances between the four groups. Translocated bilbies from both quoll-naive and quoll-exposed populations used burrows with a significantly lower number of entrances than the quoll-naive source population (quoll-naive translocated: $\beta = -0.77$ [–1.24, –0.30], $z = -3.14$, $P = 0.002$, quoll-exposed translocated: $\beta = -0.88$ [–1.35, –0.41], $z = -3.45$, $P < 0.001$, Figure 6a). Second, we looked at the probability of bilbies using a particular habitat for burrow locations (Figure 6b). Bilbies that were translocated from both control and quoll paddocks had a significant preference for using burrows in dune habitats compared with bilbies from the quoll-naive source paddock (quoll-naive translocated: $\beta = 2.43$ [0.92, 4.75], $z = 2.75$, $P = 0.002$, quoll-exposed translocated: $\beta = 1.84$ [0.21, 4.05], $z = 2.03$, $P = 0.026$). Finally, we looked at the probability that bilbies used more covered burrows (partial and full cover) between the different groups. There was a tendency for both groups of translocated bilbies to use burrows with more cover than bilbies from the quoll-naive source population (Figure 6c). Translocated bilbies from the quoll paddock were more than twice as likely to use covered burrows compared with quoll-naive source bilbies although this was not significant (Odds ratio = 2.08, $\beta = 0.73$ [–0.63, 2.09], $z = 1.06$, $P = 0.291$).

From the 30 bilbies moved to the cat-paddock, it was possible to estimate the daily distance for 26 bilbies (9F 17M) from a total of 511 recorded movements. We found mean daily distance moved between burrows was affected by sex ($\beta = 0.79$ [0.34, 1.28], $t = 3.40$, $P = 0.002$), but not by population ($\beta = 0.20$ [–0.24, 0.71], $t = 0.92$, $P = 0.408$).

We summarized the varying responses across our experiments with a focus on comparisons between populations, including effect sizes, in Table 1. The strongest effects were found for the novel pen experiment.

DISCUSSION

We used different behavioral tests to first determine if exposure to a live, native predator improved general anti-predator behaviors and then whether this exposure could also improve anti-predator behavior toward a novel predator. In Australia, native carnivores may resemble archetypes of introduced predators or introduced predator cues might be too different to elicit appropriate responses to these predators (Cox and Lima 2006). We used a range of tests to look at anti-predator responses elicited from predator models, novel environments, and live predators and found that some yielded stronger results than others.

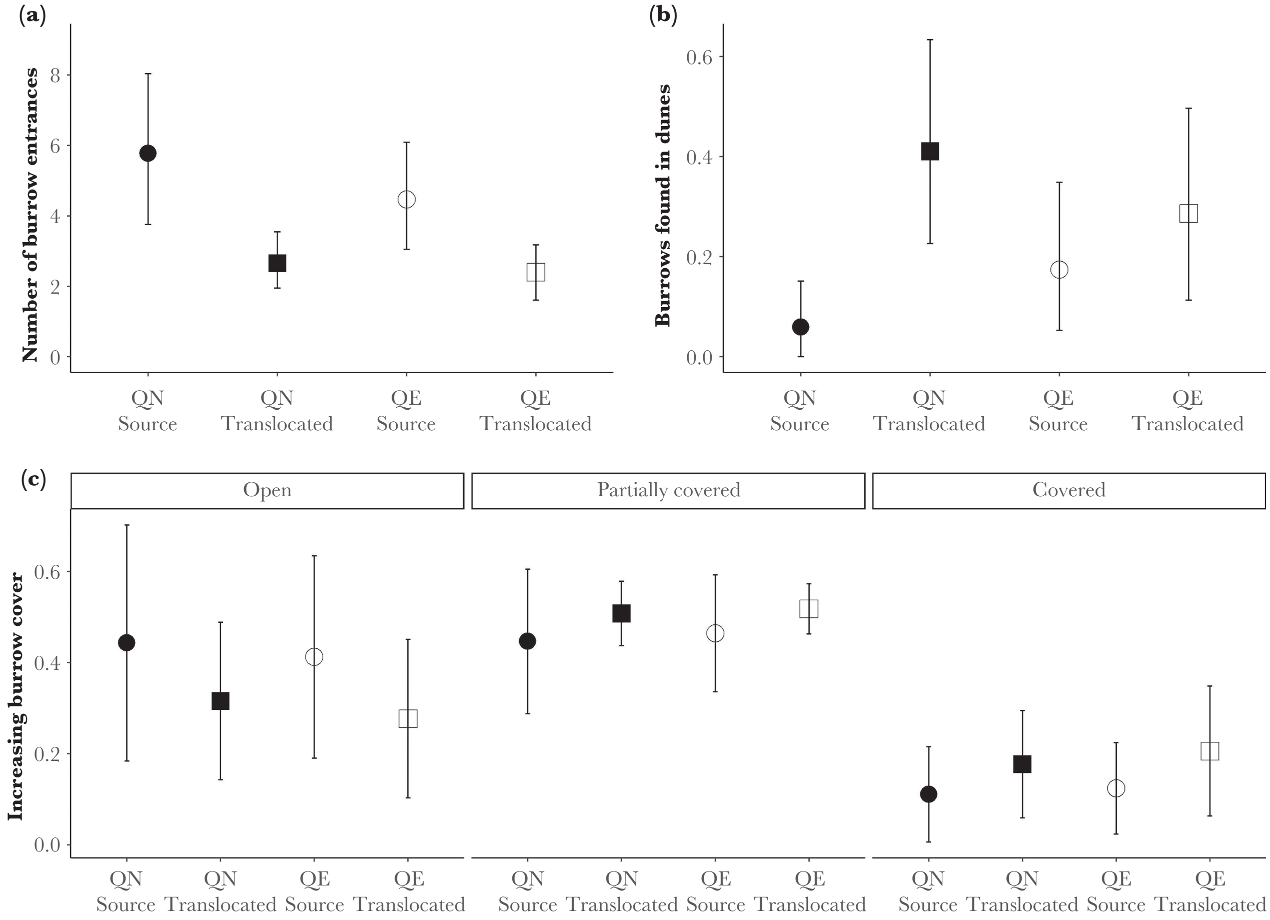

Figure 6
Burrow choice by bilbies from quoll-naive (filled) and quoll-exposed populations (open) when in source paddocks and with individuals translocated to cat-exposed paddocks. Burrow choice was defined as: (a) the predicted number of entrances per burrow, (b) probability of burrows used in dune habitat, and (c) probability of using burrows with increasing cover. Results are shown with error bars (95% confidence intervals).

Prey species may respond to general cues by predators or cues specific to a predator species to gauge risk (Sih et al. 2010). In our model experiment (Experiment 1), we had a mixed response to the models, but a weak effect of quoll-naive bilbies remaining stationary and further away from the cat model, whereas quoll-exposed bilbies remained further away and more stationary when presented with a quoll model. Time spent stationary can be a form of attentive immobility that is used to reduce potential detection by predators and to enhance perception when under threat (Lima and Dill 1990; Roelofs 2017). The limited movement by quoll-naive bilbies when presented with a cat model may be explained by bilbies processing the potential threat posed by this new and novel model species, whereas quoll-exposed bilbies appeared to recognize quolls as a predator. Although some mammals can distinguish correctly between predator and non-predator models (Blumstein et al. 2000), reactions to models can be dependent on factors such as the quality or pose of the model and the cues used by prey species. Bilbies have poor eyesight but excellent auditory and olfactory senses that may influence model response (Johnson 1989). However, we ensured that models were close to burrows to increase the chances that models were seen, and the similar response by bilbies to cat and quoll models, suggest that they could at least recognize both as potential threats by possibly position or shape. Spatial responses of bilbies to models were affected primarily by sex rather than population and follows similar findings male bilbies utilizing larger home ranges (Moseby and O'Donnell 2003). Our findings were weak and may be a consequence of the limited sample size, a challenge often encountered in trapping and monitoring threatened species.

In Experiment 2, we compared behavior and movement at burrow entrances, including the response to a live predator. Animals at risk of predation are expected to adjust their behavior to compensate for this increased risk, and this adjustment can vary depending on the level of risk they are exposed to (Lima and Dill 1990; Lima and Bednekoff 1999). In comparison to the model experiment, the presence of a live predator elicited more distinct behavioral responses. Quoll-exposed bilbies responded to live native predators that had recently been present at their burrow entrances by increasing their activity, possibly showing increased investigation to assess predation risk. Alternatively, increased activity may represent escape or avoidance behaviors (Lima and Dill 1990). The presence of live predators will naturally provide a richer stimulus and provide a range of cues, allowing prey to recognize potential threats and respond accordingly (Griffin et al. 2000), compared with other non-living cues. Using live animals, however, is logistically challenging (Griffin et al. 2000), and in our study, we took advantage of opportunistic visits by quolls recorded from passive camera videos

Table 1

Summary of general findings from each experiment comparing quoll-exposed and quoll-naïve bilbies and standardized effect sizes (95% confidence limits) for the effect of quoll-exposed populations on response variables

Experiment	Response variable	Effect size	Summary
Experiment 1: Model	Probability of moving	Bucket: 0.64 [–1.60, 2.88] Cat: 1.31 [–0.96, 3.59] Quoll: –1.29 [–3.74, 1.15] Rabbit: 0.93 [–1.55, 3.41]	Quoll-exposed population generally moved more except at quoll model
	Distance moved	Bucket: –0.29 [–1.58, 1.01] Cat: –0.76 [–2.25, 0.73] Quoll: –0.82 [–1.97, 0.33] Rabbit: –0.24 [–1.4, 0.93]	Quoll-naive population moved more in response to cat and quoll models
	Time near model	Bucket: –0.63 [–1.37, 0.11] Cat: 0.30 [–0.46, 1.07] Quoll: –0.71 [–1.54, 0.13] Rabbit: –0.06 [–0.98, 0.86]	Quoll-exposed population spent longest near cat
	Time stationary	Bucket: –0.28 [–0.94, 0.38] Cat: –0.70 [–1.55, 0.15] Quoll: 0.51 [–0.38, 1.40] Rabbit: –0.05 [–0.84, 0.75]	Quoll-exposed population paused with quoll model, quoll-naive population paused with cat model
	Time investigate model	Bucket: –0.08 [–3.32, 3.15] Cat: 2.42 [–1.18, 6.03] Quoll: –1.94 [–5.70, 1.81] Rabbit: 1.13 [–2.95, 5.21]	Quoll-exposed population investigated cat model, quoll-naïve population investigated quoll model
	Time looking model	Bucket: 0.43 [–0.56, 1.42] Cat: –0.06 [–0.59, 0.47] Quoll: –0.22 [–1.11, 0.67] Rabbit: 0.10 [–0.17, 0.37]	No strong differences between populations for any model
Experiment 2: Live predator	Time sniffing		Trend for more sniffing in quoll-exposed group after recent quoll visit
	Time stationary		Significantly less time stationary in quoll-exposed group after recent quoll visit
	Time close burrow		No strong difference
Experiment 3: Small novel pen	Latency to emerge	–0.17 [–1.04, 0.69]	No strong differences
	Time in cover	**Female: 1.01 [0.03, 1.98]** Male: –0.79 [–1.68, 0.10]	Quoll-exposed females spent more time in cover, opposite effect for males
	Time sniffing	0.18 [–0.29, 0.67]	No effect
	Time agitated	**0.47 [0.03, 0.91]**	Quoll-exposed spent more time agitated and trying to escape
	Time move fast	–0.484 [–1.15, 0.18]	No strong differences
	Time stationary	0.07 [–0.36, 0.50]	No strong differences
Experiment 4: Large Novel Pen	Daily distance	0.25 [–0.29, 0.79]	No effect
	Burrow entrances		Both populations used fewer entrances when exposed to cats
	Burrow Habitat		Both populations preferred dune habitat when exposed to cats
	Burrow exposure		Both populations preferred more covered burrows when exposed to cats

rather than direct manipulation. Unfortunately, this meant we were unable to compare the response of quoll-naive bilbies to a live native predator as no quolls were present in the control paddock.

The use of a small novel pen (Experiment 3) also successfully detected behavioral differences between the populations. Pens are often used to test behavioral responses to scent cues (Garvey et al. 2016; Stryjek et al. 2018) or novel objects (Jolly et al. 2021); however, a novel environment test in itself is less common (but see Ross et al. 2019). Novel environments can represent neophobic situations in which more-risk averse individuals are likely to respond more strongly, although neophobic responses may only be present in high-risk scenarios (Brown et al. 2013). In our small novel pen experiment with no simulated cues, we found female bilbies from quoll paddocks used vegetated environments (higher cover) more often than open ground compared with quoll-naive bilbies, but the opposite effect was found for males. Cover provides an important means of protection for vulnerable prey, and similar experiments found that bilbies from cat-exposed treatments spent more time in cover than predator-free bilbies (Ross et al. 2019). Quoll-exposed bilbies also spent more time engaged in agitated or escape behaviors than quoll-naive bilbies. Bilbies have highly developed olfactory senses (Johnson 1989), and prior exposure to predators may have increased their response to other predators (e.g., Ferrari et al. 2007). Wariness and neophobia are traits that can be important for reducing risk, and neophobic responses have been found in other prey species exposed to quolls (Jolly et al. 2021). Testing individual behavior in novel pens may be a useful mechanism for selecting individuals for translocation and increased survival in predator areas (Moseby et al. 2016).

These first three experiments suggested that bilbies previously exposed to quolls appeared to show some recognition and response to quoll models and the presence of a live quoll. The novel pen trial and live predator presence stimulated the strongest responses during our trials, suggesting that using artificial predator cues such as models may have limited value. While our results did show some level of inconsistency, likely resulting from low sample size in some cases, there was some indication that quoll-exposed bilbies were generally warier and neophobic than quoll-naive bilbies. As hypothesized, these results would indicate that survival of quoll-exposed bilbies should be enhanced when exposed to novel predators.

We then tested whether exposure of native prey to native predators could act as a stepping stone to improving responses to novel predators, but found limited evidence to support this hypothesis. In Experiment 1, quoll-exposed bilbies did not significantly change their behavior toward cat models compared with quoll-naive bilbies, although there was a weak effect of quoll-exposed bilbies moving less and spending longer near the cat and quoll model than the quoll-naive bilbies. In Experiment 4, moving quoll-exposed and quoll-naive bilbies to a large paddock where live novel predators were present initiated a similar change in behaviors in both populations. Bilbies from both source populations used burrows with fewer entrances after release and chose burrows more often in dune environments.

These findings suggest that exposure to native carnivores did not confer additional advantages when faced with a novel predator. While this result may not be surprising in the context of mammal extinctions in Australia, where quolls have previously co-existed with many prey species, this coexistence was at the continental scale, and may not have been the case in many local areas. Additionally, quoll exposure in pre-European Australia may well have conferred an initial advantage when introduced predators arrived, but high-predator abundance supported by the hyperabundance of introduced rabbits in the early years of European settlement may have limited this advantage. Interestingly, in a previous study, bilbies trained to fear predators used burrows with more entrances and moved further distances between burrows than quoll-naive bilbies after training (Moseby et al. 2012). However, no difference was found in burrow choice once both populations of bilbies were translocated to a novel area with predators, similar to our findings.

These results may be due to several factors. First, bilbies may exhibit a strong innate response to novel environments, causing both populations to change their behavior after release into a novel environment (Moseby et al. 2012). However, this does not explain the differences in behavior recorded during the small novel pen test in Experiment 3. Alternatively, the period of prior exposure to quolls may have been insufficient or density may not be high enough to elicit behavioral responses (Cunningham et al. 2019). However, this is unlikely as long-term track counts showed low but consistent quoll tracks in these paddocks, and quoll scats have been found to contain the remains of bilbies (Arid Recovery, unpublished data), suggesting predation was a real threat. It is also possible that our behavioral tests may have been inappropriate. Cat predation risk may also have been too low in the cat paddock as evidenced by the survival of all bilbies released. Finally, quoll exposure may not induce appropriate responses to cats due to dissimilarities in hunting styles, particularly as cat hunting behavior is more intensive than in some species of quolls (Hamer et al. 2021). Quolls and cats are only distantly related and may not share sufficient similarities in their predatory cues and/or behavior to support such a learning transfer. However, given high cat predation pressure or further ontogenetic experience with cats beyond the three months we tested, perhaps the advantage of quoll exposure would be more evident. Comparing survival rates of bilbies between quoll-exposed and quoll-naive populations would be the optimum way to test this stepping stone hypothesis but cat predation risk for bilbies during our study was low, likely due to the presence of an unusually high abundance of alternative cat prey (rodents) during our experiment (Arid Recovery, unpublished data). Since bilbies are known to be preyed on by cats (Moseby et al. 2011; Berris et al. 2020), studying anti-predator responses under increased predation risk would be necessary to fully resolve some of these issues.

Finding appropriate solutions to eliminate predator naiveté is an important ongoing challenge. Currently, there is encouraging evidence that direct exposure to live but low-density predators, in situ predator conditioning, is allowing prey species to learn and develop anti-predator responses (Gerard et al. 2014; Moseby et al. 2018; Blumstein et al. 2019). In situ training using native carnivores rather than novel predators has the advantage of providing opportunities for conservation of these predator species while also possibly improving anti-predator traits in prey. Recent in situ studies of reintroducing native carnivores like the Tasmanian devil *Sarcophilis harrisii* and northern quoll *Dasyurus hallucatus* have shown rapid adjustment of behavior in prey species to be more predator savvy (Cunningham et al. 2019; Jolly et al. 2021) and similar changes have also been found in non-mammalian species (Lapiedra et al. 2018). If these traits could also enhance the survival of prey exposed to novel predators, then this would be an added benefit to species conservation initiatives. Such long-term strategies may be one of the few ways to encourage coexistence with invasive species (Evans et al. 2022). Where conservation of some species is prioritized to fenced reserves, for example, for highly endangered species or those particularly vulnerable to predation, the use of native rather than novel predators may provide an important mechanism to develop anti-predator traits. While our results show some promise in detecting differences in vigilance and neophobic behavior when using native species as a training tool, when bilbies were faced with novel predators it was less clear if native predators provided an advantage, and thus their use as a “stepping stone” to improving responses to novel predators is unclear. The range of predator cues we tested to elicit anti-predator responses appeared to vary with the strength of the cue and the real risk posed to prey. In other studies, variable risk level was suggested to be responsible for differing spatial avoidance of predators in two reptile species (Gerard et al. 2014). Even if anti-predator traits have improved, designing experiments to test for these is challenging because inappropriate cues are unlikely to trigger a response (Sih et al. 2010; Carthey and Banks 2014). Consequently, cue choice is important, particularly when assessing the value of experimental manipulations used to reduce the impact of prey naivety.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

This project was conducted under ethics approval by the Animal Care and Ethics Committee of UNSW (20/109A). The study was supported by Arid Recovery. The authors would like to thank the staff at Arid Recovery, B. Stepkovitch, C. Arkinstall, B. Coulter, S. Gerhardy, T. Berthold, E. Reynolds, T. Manning, H. McGregor, A. Nielson, C. Bruinsma, L. Jokinen, E. Pollard, A. Marinelli, M. Humphries, K. Matthews and B. Cox for field assistance with capture, monitoring and tracking of bilbies. The authors also acknowledge the Kokatha people as the Traditional owners of the lands on which this research was undertaken. The authors would like to thank two anonymous reviewers for providing expert advice to improve this manuscript.

FUNDING

This work was supported by the Australian Research Council Linkage Project (LP190100291)

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Van der Weyde et al. (2022)

CONFLICT OF INTEREST

The authors declare no conflict of interest for this study.

Handling Editor: Ulrika Candolin

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