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RESEARCH ARTICLE

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Reversing the effects of evolutionary prey naiveté through controlled predator exposure

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Abstract

1. Inappropriate anti-predator responses (naiveté) towards introduced predators is a key factor contributing to the extinction and endangerment of prey species world-wide and the failure of wildlife reintroductions. Here, we test the idea that success of reintroduction can be improved by exposing a predator naïve prey species to introduced predators under controlled conditions (in situ predation) prior to reintroduction, such that prey adopt increased wary behaviours to aid in survival.
2. We exposed a population of a naïve marsupial, the greater bilby (*Macrotis lagotis*), to a controlled number of introduced predators (feral cats, *Felis catus*) for 2 years within a large fenced paddock and then compared the pre-release behaviour and post-translocation survival of predator-exposed and predator-naïve bilbies over 40 days.
3. Behavioural assays conducted in a small pen prior to reintroduction suggested that predator-exposed bilbies were warier as they spent less time moving and more time in cover than predator naïve bilbies.
4. After translocation, predator-exposed bilbies were more likely to survive to 40 days and were less likely to be preyed upon by cats than predator-free bilbies.
5. *Synthesis and applications*. Naiveté towards predators is a major problem thwarting successful reintroductions world-wide. Our study demonstrates that exposure to predators under controlled conditions can increase survival of reintroduced prey and is a promising approach to overcome the problem of naiveté towards introduced predators and the global problem of prey naiveté. Future conservation of naïve prey species may depend on such training methods prior to releasing into areas where predators are present.

KEYWORDS
anti-predator behaviour, Australia, controlled exposure, feral cat, greater bilby, predator training, prey naiveté, reintroduction

1 | INTRODUCTION

Populations of species that encounter introduced predators or have been isolated from predators for extended periods often have ineffective predator avoidance strategies, making them particularly susceptible to predation (Berger, Swenson, & Persson, 2001; Carthey & Banks, 2014). Such 'prey naiveté' is a major cause of species decline world-wide (Salo, Korpimäki, Banks, Nordström, &

Dickman, 2007; Sih et al., 2010). Naiveté is particularly problematic on islands, where species have persisted in the absence of predators but have subsequently been wiped out after the introduction of a novel predator (Blackburn, Cassey, Duncan, Evans, & Gaston, 2004). Prey naiveté is common in species with no evolutionary history of exposure to predators (e.g. Carthey & Blumstein, 2017; Griffin, Blumstein, & Evans, 2000; Woinarski, Burbidge, & Harrison, 2015), but can also be acquired if predators are removed for an extended period (ontogenetic evolution; Berger et al., 2001; Jolly, Webb, & Phillips, 2018). In Australia, evolutionary naiveté towards introduced predators, the feral cat (*Felis catus*) and red fox (*Vulpes vulpes*), is thought be a key factor responsible for the extinction and endangerment of native rodents and marsupials (Moseby, Blumstein, & Letnic, 2015).

Species that have declined to a few small remnant populations are at a higher risk of extinction (Brooks et al., 2002), thus, translocations are undertaken in an attempt to establish additional populations in historical or new ranges. These translocations are often unsuccessful (Short & Smith, 1994), and prey naiveté may be a key factor in failures. Only 32% (123 out of 380) of Australian translocations between 1880 and 2009 were successful, and predation by introduced predators contributed to 80% of failed mammalian translocations (Moseby et al., 2011). Fenced reserves and sanctuaries are often built to exclude predators and protect the species within. Despite best intentions, these ‘mainland islands’ may exacerbate prey naiveté by isolating prey from their predators and driving the further loss of anti-predator behaviour (Jolly et al., 2018; Moseby, Blumstein, et al., 2015).

To combat the problem of prey naiveté, studies have attempted to ‘train’ naïve individuals to recognize predators and engage in anti-predator behaviour. The most common training methods pair a predator cue with a negative event (Griffin et al., 2000). For example, pairing a predator odour with a chemical alarm signal (e.g. Brown & Smith, 1998; Magurran, 1989); a stuffed predator with either a simulated attack (e.g. Griffin, Evans, & Blumstein, 2002; McLean, Schmitt, Jarman, Duncan, & Wynne, 2000; Miller et al., 1990; Paulino, Nogueira-Filho, & da Cunha Nogueira, 2018; Teixeira & Young, 2014) or a recorded alarm call (e.g. Lundie-Jenkins, 1996); or a combination of cues and events (e.g. McLean, Hölzer, & Studholme, 1999; Moseby, Cameron, & Crisp, 2012; White, Collazo, & Vilella, 2005). While experiments designed to overcome the problem of prey naiveté have demonstrably modified behaviour, the benefits in terms of survival are less clear. Most studies have either not determined whether trained behaviours had any effect on subsequent survival, have found no difference in survival between trained and control individuals (e.g. Moseby et al., 2012), or failed to compare trained individuals with a control (e.g. White et al., 2005). The failure of these experiments suggests that traditional associative learning methods using models and other surrogates for live predators may not adequately prepare animals for surviving with live predators upon release (Seddon, Armstrong, & Maloney, 2007).

Training programs that use real predation experiences show more promise. One study in the USA used predator-exposed adult black-tailed prairie dogs (*Cynomys ludovicianus*) to train naïve juveniles in the absence of predators, and found that survival of trained juveniles was not different to survival of wild-raised individuals, but significantly better than juveniles trained without an experienced adult (Shier & Owings, 2007). Another successful study in Saudi Arabia used a live muzzled fox or a control model fox with either live or recorded houbara bustard (*Chlamydotis [undulata] macqueenii*) alarm calls to induce anti-predator responses in captive-bred houbaras before release into the wild. Houbaras only showed survival improvement if exposed to the live predator, not the model (Van Heezik, Seddon, & Maloney, 1999). These successful studies suggest that anti-predator behaviour can be learned, but requires training reflective of real-world risk.

Moseby, Blumstein, et al. (2015) proposed a novel method, in situ predation, to improve the anti-predator responses of predator naïve prey prior to reintroduction. The proposed method involves exposing populations of naïve prey to low densities of introduced predators over extended time periods in order to ‘fast-track’ learning and co-evolution. Initial results from in situ predator trials suggest that significant changes in behavioural and physical traits can be stimulated through exposure to predators (Moseby, Letnic, Blumstein, & West, 2018a; West, Letnic, Blumstein, & Moseby, 2018).

In this study, we contrast the behaviour of a predator naïve population of greater bilbies (*Macrotis lagotis*) with one that has lived with low densities of predatory feral cats for 2 years, and then quantify survival when individuals from both populations were subsequently translocated to an area with a high density of feral cats. If predator-exposed bilbies were less naïve we predicted that they would: (a) spend a larger proportion of time exhibiting wary behaviours and using available cover; (b) have more burrows and move burrows more often as a way to avoid cats (as per Moseby et al., 2012) and (c) have greater survival compared to predator-free bilbies when exposed to a higher density of feral cats. Our results have significant implications for improving the success of global reintroductions and restoration projects into areas where predators are present.

2 | MATERIALS AND METHODS

2.1 | Study species

The greater bilby is a nocturnal marsupial native that once roamed over 70% of the Australian mainland. Males weigh up to 2.5 kg and females around 1 kg (Johnson, 2008). They forage for food at night (predominantly seeds and insects; Gibson, 2001) and during the day they shelter in burrows. Bilby home ranges include multiple burrows which can be up to 4.5 m long and 2 m deep with spirals and side branches (Johnson, 2008).

The bilby is listed as vulnerable globally (IUCN red list) and nationally under the Australian Government EPBC Act (Johnson, 2008). Predation by feral cats and foxes is thought to be largely responsible for their continuing decline (Johnson, 2008). In 2016 Arid Recovery Reserve had a population of approximately 500 bilbies which were the progeny of 67 individuals released between 2000 and 2005 (Moseby et al., 2011).

2.2 | Study location

The Arid Recovery Reserve (30°23′S 136°54′E) is a 123 km^2 network of fenced exclosures situated 20 km north of Roxby Downs in arid South Australia. Several locally extinct species have been reintroduced into the Reserve, including the vulnerable greater bilby (Moseby et al., 2011). The reserve is divided into paddocks (see map Supplementary Material S1); this study was conducted in three paddocks: the predator-free paddock (14 km^2), the predator-exposed paddock (26 km^2), and the release site (37 km^2).

The predator-free paddock has been free of feral predators since 1998. The predator-exposed paddock had one resident cat until 2015, when four desexed males and one female were additionally released into the paddock to examine the effect of low-level predator pressure on native species (Moseby, Letnic, Blumstein, & West, 2018b; Moseby et al., 2018a). Total cat numbers fluctuated between 0.04 and 0.35 cats/km^2 (Moseby et al., 2018b). Exact bilby density is unknown, but infrared cameras show an increase in bilby numbers since introduction (Moseby et al., 2018b). Pre-exposure of bilbies to cats may have led to an improvement in anti-predator behaviour of individuals but also the removal of the more naïve individuals through cat predation. Cat-driven mortality of bilbies in the predator-exposed paddock is unknown, but since initial release in 2015, cat predation of bilbies has been confirmed from the presence of bilby remains in cat scats and stomachs (Moseby et al., 2018b).

Both the predator-free and predator-exposed paddocks contained bilbies, as well as reintroduced burrowing bettongs (*Bettongia lesueur*), plains mice (*Pseudomys australis*) and spinifex hopping mice (*Notomys alexis*). The predator-exposed paddock contained low densities of European rabbits (*Oryctolagus cuniculus*). The predator-free paddock is generally rabbit-free although incursion has infrequently occurred in the past. Sand goannas (*Varanus gouldii*) occur in all paddocks, but do not share burrows with bilbies (Read & Scoleri, 2015). Sand goannas have shown no tendency to prey on bilbies in any previous releases at Arid Recovery (e.g. Moseby & O'Donnell, 2003; Moseby et al., 2011).

The release paddock contained no bilbies, bettongs or bandicoots but had both mice species as well as European rabbits, which were culled to low densities in the month prior to this experiment. Camera traps were used across the reserve to confirm that no other feral predator invasions (cats, red foxes or dingoes; *Canis lupus dingo*) occurred during the study period (Moseby et al., 2018a).

2.3 | Behavioural trial of predator-exposed and predator-free bilbies

We compared the behaviour and cover use of bilbies from the predator-free and predator-exposed populations prior to release by conducting a behavioural assay in a small fenced pen (10.8 × 4.8 m) (see map Supplementary Material S1). The walls of the pen were made of wire mesh and had two layers of shade cloth attached to them to ensure no visibility into or out of the pen from ground level. One quarter of the pen contained vegetation suitable for seeking shelter, and the remaining three quarters were covered in bare sand with no shelter (see pen image Supplementary Material S2). A 15-cm diameter PVC pipe was used to create an artificial bilby burrow in the centre of the pen. The pipe was partially buried and lined with soil to mimic a real burrow. A right-angle entrance was cut into the pipe and faced towards the relative safety of the available vegetation cover. A hessian cloth cover was attached to the burrow entrance with a pulley, such that an observer could expose the entrance from outside the pen.

In May 2017, we captured 36 bilbies from Arid Recovery for behaviour comparisons; 20 from the predator-free population, and 16 from the predator-exposed population. Bilbies were trapped in cage traps ($n = 5$) or by hand using handheld nylon fishing nets ($n = 31$), as described in Moseby et al. (2012). Bilbies were kept in thick fleece bags away from potential sound and light stressors for 1 hr before behavioural experiments to reduce any differences in capture anxiety between individuals. Bilbies were then individually transferred to the artificial burrow by placing the bag opening over the burrow, pushing the bilby into the burrow and placing the cover over the entrance without allowing the bilby to see the pen or handlers. Individuals were allowed to acclimatize in the burrow for 5 min before the cover was removed by drawing on the pulley and exposing the burrow entrance. A single observer sat quietly behind a hide outside the pen and operated the pulley whilst using a night vision video camera (Pulsar Recon 550R 4 × 50) to observe the time taken to emerge from the burrow. The observer then filmed the behaviour of the bilby for 15 min following emergence. Observation ended after 15 min following emergence, or after 30 min of no emergence, at which point emergence time was listed as 30 min and no post-emergence behaviour was recorded (right censored). All observations and recordings were made by a single observer, with no other people or light sources in the vicinity. Bilbies were then removed from the pen and returned to their capture location. We used a Cox regression to determine whether the time taken to emerge from the shelter during the trial was independent of treatment (predator free/predator exposed).

Videos of the bilbies after emergence were scored using the event-logging software BORIS v4.1.4 (Friard & Gamba, 2016) to determine the proportion of time that they allocated to behaviours (moving [fast/medium/slow], stationary [bipedal/quadrupedal] or investigative [exploring fence with nose]; see full ethogram Supplementary Material S3); and videos were also scored for cover use (vegetation/bare sand) independent of behaviour categories, since predation risk has historically been shown to increase wariness, reduce movement and reduce feeding in open areas (Jolly et al., 2018; Sih & McCarthy, 2002; West et al., 2018). All videos were scored blind by the same observer. Three recordings were shortened and one recording excluded due to equipment error. To determine whether predator-free and predator-exposed bilbies behaved differently, and whether behaviours changed over time, we entered each response (behaviour:

moving, stationary, investigative and cover use: vegetation/bare sand) as a continuous response variable (normal distribution with identity link function) into separate generalized linear mixed models (GLMMs) with treatment (predator free/predator exposed) time interval (0–5 min/5–10 min/10–15 min) and the interaction between treatment and time interval as fixed factors. Because our analysis involved repeated measures of individuals over three time intervals, time was treated as a repeated measure using a compound symmetry covariance error structure. Pairwise contrasts were done to identify differences between treatments by interval. Statistical analyses were performed using IBM SPSS Statistics for Windows, v25 (IBM Corp., Armonk, NY, USA).

2.4 | Behaviour and survival following release

To conduct an experimental test of the effects in situ predation had on the survival of reintroduced prey, we took bilbies from the predator-free paddock and the predator-exposed paddock and introduced them into the release paddock where a higher density of cats were present.

Over 3 weeks in June 2017, 48 bilbies were captured using spotlights and handheld nylon fishing nets as per Moseby et al. (2012), and translocated to the release site: 24 from the predator-free population, and 23 from the predator-exposed population. Radio transmitters with whip antennae (Sirtrack 45 g with a mortality indicator) were attached to the tails of 21 bilbies from each population (*n* = 42 total). Five bilbies were not given radio transmitters because they weighed less than 450 g. Transmitters were attached to shaved areas on the tails using veterinary grade tape, as per Moseby and O'Donnell (2003). Extra care was taken to ensure that the transmitter was not firmly pressed to the tail to prevent the formation of tail ulcers. Bilbies were kept in pet packs on site the day following capture and provided with water and grain before being released at dusk, such that no bilby was kept for longer than 24 hr. Pet packs were kept in a dark, cool room with no outside noise to reduce stress. Bilbies were released into pre-existing rabbit warrens in the release site, not more than 0.5 km from the main water source. Release warrens were selected randomly for each bilby regardless of treatment.

The 42 bilbies with transmitters were tracked daily for up to 40 days. Since release was staggered, this meant between 6 and 37 bilbies were tracked at a time (median = 24). Burrow use was recorded for the first 3 weeks to compare the average number of burrows used, and the number of times bilbies within the two treatments changed burrows, since predator wariness has been linked to increased refuge use (Krivan, 1998) and regular burrow movement (Moseby et al., 2012). We also recorded ‘share events’, that is when individuals shared burrows with other bilbies. Tracking ended before 40 days when transmitters fell off (right censored; *n* = 12), or when bilbies died (*n* = 14). Bilbies were removed from the study after the last known status as per survival analyses, such that those still being tracked on the final day were marked ‘alive’ (right censored; *n* = 16). Burrow use was determined by dividing the total burrows used by the number of days an individual was radio-tracked to their burrow to account for differing survival. Individuals were included only if they used a burrow other than their release burrow before an end event (predation or fallen transmitter) (*n* = 9 excluded). A generalized linear model (GLM) was used to test whether burrow use was influenced by predator exposure. Average number of burrows and share events per radio-tracking day were entered as dependent variables, with treatment as the fixed factor. A normal distribution with an identity link function was used for analyses.

The radio transmitter mortality indicator was activated after 12 hr without movement, and when this occurred bilbies were located and their remains retrieved. Cause of death was consistent with cat predation and confirmed with nearby tracks and cat traces, such as scats, carcass wounds (e.g. removal of head) and cat prints alongside prey ‘drag marks’ (i.e. the track left by the cat dragging the carcass across the ground). Fourteen carcasses were retrieved and swabbed for DNA analysis and sent to Helix Molecular Solutions to test for the presence of cat DNA (see method Moseby, Peacock, & Read, 2015).

Remaining bilbies were not monitored after 40 days but were checked at 2 months to confirm all transmitters had fallen off naturally. We used a Kaplan–Meier estimate with a Weibull hazard model to determine the effect on survival. This analysis was performed in R v3.5.2 using the survival package v 2.38 (Therneau & Grambsch, 2000).

Research was conducted with animal ethics approval from the South Australian Wildlife Ethics Committee; approval no. 1/2014M2.

3 | RESULTS

3.1 | Behavioural trial of predator-exposed and predator-free bilbies

Although predator-exposed bilbies took longer on average to emerge from the burrow than predator-free bilbies (16.48 min and 10.85 min, respectively), emergence time was non-significant for treatment (Cox regression, $\chi^2_1 = 1.121$, $p = 0.290$), with 85% of predator-free bilbies emerging within 30 min compared to 63% of predator-exposed bilbies.

After bilbies had emerged from the artificial burrow, treatment by itself did not explain variation in the proportion of time spent moving, investigating, remaining stationary, or under cover. However, interval significantly explained movement, investigation and cover use, and the interaction between treatment and interval significantly explained movement and investigation (Table 1).

Contrasts of behaviours revealed that predator-free bilbies allocated a larger proportion of time to movement and use of bare sand habitat in the first interval (0–5 min), but a similar proportion of time to stationary and investigative behaviours compared to predator-exposed bilbies. In the second interval (5–10 min) predator-free bilbies allocated a larger proportion of time to movement but not investigation, stationary or cover use compared to predator-exposed bilbies.

TABLE 1 Results of GLMMs main effects for each behaviour. Treatment = predator exposed/predator free. Interval = 0–5 min, 5–10 min, 10–15 min. Statistically significant results have been shaded ($p < 0.05$). For all GLMMs: error distribution = normal, link function = identity

	Main effect		
Behaviour	**Treatment**	**Interval**	**Treatment*Interval**
Moving	$F_{1,28} = 4.128$ $p = 0.052$	$F_{2,68} = 7.572$ $p = 0.001$	$F_{2,68} = 7.841$ $p = 0.001$
Investigative	$F_{1,19} = 0.460$ $p = 0.506$	$F_{2,58} = 3.452$ $p = 0.038$	$F_{2,58} = 5.130$ $p = 0.009$
Stationary	$F_{1,16} = 0.242$ $p = 0.630$	$F_{2,32} = 0.078p = 0.925$	$F_{2,32} = 1.301$ $p = 0.286$
Cover Use	$F_{1,29} = 1.079$ $p = 0.308$	$F_{2,42} = 5.300$ $p = 0.009$	$F_{2,42} = 2.784$ $p = 0.073$

In the third interval (10–15 min), predator-free and predator-exposed bilbies allocated a similar proportion of time to all activities (Table 2; Figure 1).

TABLE 2 Results of contrasts of GLMMs for each behaviour over the three time intervals for each treatment: predator free/predator exposed. Statistically significant results have been shaded ($p < 0.05$). For all GLMMs: error distribution = normal, link function = identity

	Interval		
Behaviour	**0–5 min**	**5–10 min**	**10–15 min**
Moving	$F_{1,27} = 12.117$ $p < 0.001$	$F_{1,25} = 4.333$ $p = 0.046$	$F_{1,24} = 1.066$ $p = 0.341$
Investigation	$F_{1,16} = 2.031$ $p = 0.173$	$F_{1,23} = 3.037$ $p = 0.095$	$F_{1,15} = 2.212$ $p = 0.157$
Stationary	$F_{1,8} = 0.505$ $p = 0.498$	$F_{1,23} = 0.398$ $p = 0.534$	$F_{1,10} = 0.490$ $p = 0.500$
Cover Use	$F_{1,28} = 9.146$ $p = 0.005$	$F_{1,16} = 0.391$ $p = 0.541$	$F_{1,27} = 0.564$ $p = 0.459$

3.2 | Burrow use post release

There was no difference in the number of unique burrows used by bilbies in either treatment (Wald $\chi^2_1 = 0.112$, $p = 0.738$), but predator-exposed bilbies were more likely to share a burrow than predator-free bilbies (Wald $\chi^2_1 = 5.932$, $p = 0.015$; Figure 2). Sex did not influence burrow sharing (Wald $\chi^2_1 = 0.013$, $p = 0.911$) but females used fewer distinct burrows than males (an average of 3.9 compared to 4.9, respectively; Wald $\chi^2_1 = 5.517$, $p = 0.019$).

3.3 | Survival

In the first week following release, there was a high rate of mortality for both predator-free and predator-exposed bilbies (43% and 14%, respectively) but mortality was higher in predator-free bilbies. There was a difference in survival over the entire 40-day experiment among treatment groups (Kaplan–Meier; $\chi^2_1 = 4.15$, $p = 0.042$; Figure 3). Of the bilbies with known fates, there was a 71% mortality in predator-free bilbies and 33% mortality in predator-exposed bilbies. All bilby mortalities were consistent with cat predation and cat DNA was present on all analysed carcasses ($n = 14$).

4 | DISCUSSION

Our results show that predator-exposed bilbies moved less, spent more time in vegetation cover, shared burrows more often and had lower mortality than predator-free bilbies. We found that exposure of bilbies to feral cats at a low density over an extended period of 2 years was sufficient to modify behaviour and improve post release survival outcomes. This finding is significant because it is the first experimental test of in situ predator exposure and shows that the fate of animals subsequently introduced into a predator-rich environment could be explained specifically by prior experience living with predators. Previous training experiments using predator cues (e.g. auditory, olfactory or visual) demonstrably modified behaviour but not survival (e.g. Moseby et al., 2012) providing no indication that predator cues reduced prey naiveté to such an extent as to improve survivorship after exposure to real predation risk.

Despite the small sample size, we found improved survival in predator-exposed bilbies. Our results together with the increased survival found in other experiments (e.g. Shier & Owings, 2007; Van Heezik et al., 1999) suggest that live predator exposure can improve post-release survival where enhancing recognition alone may be ineffective. Given the extent of past reintroduction failures due to predation (e.g. Moseby et al., 2011; Short & Smith, 1994), live predator exposure may need to become an increasingly important aspect of conservation programs to ensure reintroduction success of naïve prey species.

In this study, predator-exposed bilbies allocated a smaller proportion of time to movement and spent more time under vegetation cover during the first 5 min following emergence from their burrows. This is consistent with the hypothesis that predator-exposed bilbies were warier than predator-free individuals. Previous studies have shown that increased individual movement is associated with decreased wariness (Lima, 1998; Lima & Dill, 1990; Sih, 1987). The reduced time predator-exposed bilbies allocated to movement may thus reduce susceptibility to cat predation because cats are visual and auditory predators that use movement as a cue to locate their prey (May & Norton, 1996). Increased allocation of time spent in vegetation cover is also linked to increased wariness, since open habitats

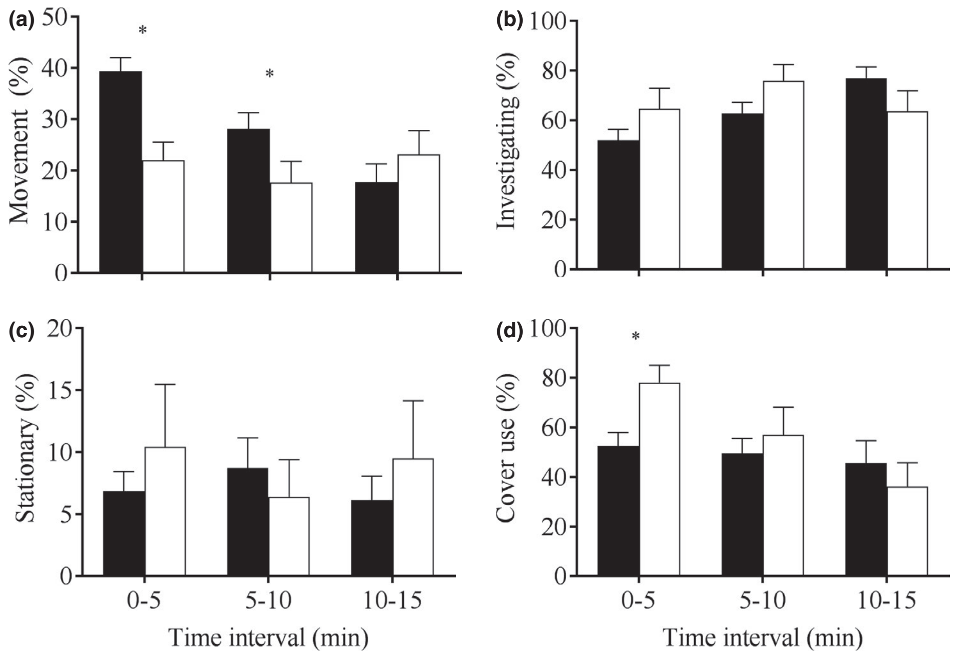

FIGURE 1 Mean time (±1 *SEM*) allocated to (a) movement, (b) investigation (c) stationary behaviours, and (d) vegetation cover use for predator free (■) and predator exposed (□) bilbies over three time intervals. * denotes statistical significance ($p < 0.05$)

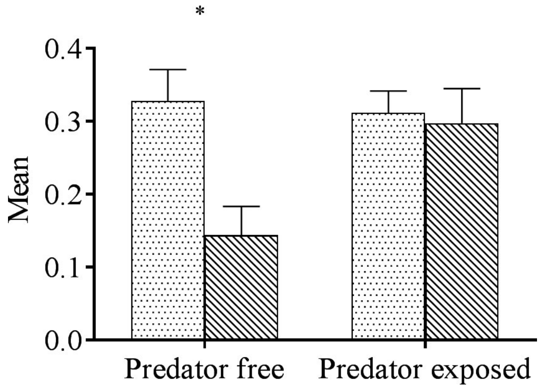

FIGURE 2 Mean (±1 *SEM*) number of burrows (▒) and share (▧) events per day for the treatments. * denotes statistical significance ($p < 0.05$)

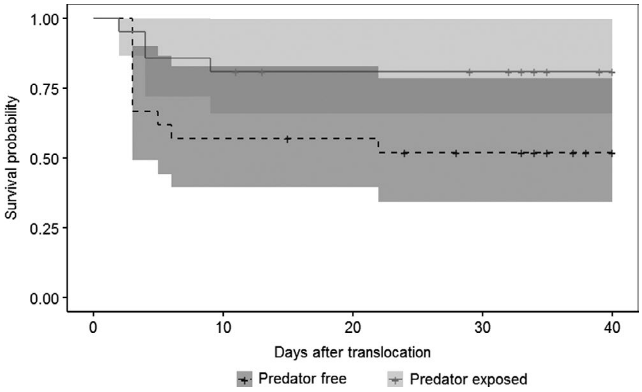

FIGURE 3 Survival comparison between the predator-exposed and predator-free groups over 40 days. Censorship shown as line ticks. Individuals were censored if tracking ended before the completion of the study (i.e. due to transmitter falling off). The predator-exposed group had a significantly greater survival than the predator-free group (Kaplan–Meier with Weibull distribution; $\chi^2_1 = 4.15$, $p = 0.042$, 95% CI)

are areas of higher predation risk in many species as they can lead to higher detection rates by predators (Creel & Winnie, 2005).

Interestingly, the magnitude of the differences between predator-exposed and predator-free bilbies decreased during the time course of the behavioural assay and there were no differences in behaviour or cover use in the final (10–15 min) time interval. Increased vigilance reduces the amount of time available for other activities (Olson, Haley, Dyer, & Adami, 2015), so the observed change may reflect that wary behaviour is suppressed when no threats are observed, thus permitting more time to allocate to other activities. Additionally, predator encounters are usually short-lived and so the behavioural response of prey to a stressor (such as a possible predation event or, here, release in an unknown environment) is likely to be strongest in the first few minutes after an encounter, followed by a gradual return to non-defensive behaviours (Blanchard, Blanchard, Rodgers, & Weiss, 1990). Future behavioural studies could reduce trial times by focusing only on the initial behaviours post-emergence to detect the strongest differences in wariness.

Following release, we expected predator-exposed bilbies to use more burrows than bilbies from the predator-free population as other studies have found increased movement between shelter sites may be a response to higher predation risk (Dill, 1987; Moseby et al., 2012). However, there was no difference in the number of burrows used between the treatments, suggesting that prior exposure to predators does not affect burrow use.

An unexpected finding was that predator-exposed bilbies were more likely to share burrows than predator-free bilbies. Burrow sharing may reduce predation risk; indeed, increased group size is commonly seen in non-solitary species when predator pressure is high (Roberts, 1996). We suggest that future studies investigate the relationship between burrow use and wariness, since our findings and others suggest this could be an anti-predator behaviour that affects survival post-translocation (Moseby et al., 2012; Robley, Short, & Bradley, 2002).

The first days and weeks of a reintroduction or translocation program are the most important because individuals must establish new territories and home ranges in an unknown area (Janmaat, Olupot, Chancellor, Arlet, & Waser, 2009; Kemp, Norbury, Groenewegen, & Comer, 2015; Wolf, Frair, Merrill, & Turchin, 2009). Anything that can reduce mortality at the start of a reintroduction program may increase the ultimate success of that program. Indeed, both treatments in this experiment showed increased mortality in the first week following release, but predator exposure appears to reduce this effect. Our research provides evidence that predator exposure improves survival in the first 40 days following translocation, and thus that in situ predator training may give predator naïve species a vital edge that increases the chance of creating a sustainable population in areas with some predators.

Though this research does not distinguish between plastic (i.e. learned) and evolved behavioural responses, future research may benefit from differentiating between the two by comparing behaviour pre- and post-release into a predator area, to determine whether behaviour modification is caused by selective predation targeting risk-prone individuals, versus being a learned factor caused by predator exposure. Additional research may also determine if survival success continues after the initial 40-day post-release time-frame, and if longer exposure to cats prior to release magnifies or extends survival differences. Unfortunately, due to the difficulties in attaching transmitters to bilbies for long periods, we do not have detailed data on subsequent individual survival as a function of predator exposure. However, our research provides promising evidence that survival in the important first weeks after translocation can be improved, thus improving the future survival of a naïve population in an area with predators.

We caution that in situ predator exposure may not be an appropriate strategy for all potentially naïve prey, especially those that have had very long periods of isolation from predators and smaller species that are more susceptible to predation. Indeed, for some populations, the training 'cost' (i.e. the number of individuals lost during predator exposure) might be too high to be an effective strategy. A potential solution could be to expose a subset of a population to predators, thus inducing or creating predator avoidance strategies, before returning the trained individuals to the main population. This could potentially spread the genes or behaviours to a larger number of individuals without risking the entire population.

Our study demonstrates that some predator-naïve species can benefit from controlled long-term exposure to introduced predators in order to change behaviour and improve survival. This may have significant implications for the conservation of species that have not co-evolved with introduced predators or have been excluded from predators for extended periods. In particular, our results may be useful for improving captive breeding and reintroduction programs by providing an important additional step between captive breeding and full-scale release. Exposure to controlled levels of real predators is likely to be more effective than attempting to predict and mimic appropriate predator cues to 'train' species.

ETHICS

Research approved by the South Australian Wildlife Ethics Committee; approval no. 1/2014M2.

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AUTHORS' CONTRIBUTIONS

K.E.M. and A.K.R. designed the project with significant contributions from M.L. and D.T.B.; data collection was conducted by A.K.R. and K.E.M. All the authors assisted in data analysis; A.K.R. wrote the manuscript with contributions from K.E.M., M.L. and D.T.B. All the authors contributed critically to the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.gv7827s (Ross, Letnic, Blumstein, & Moseby, 2019).

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