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Predator exposure improves anti-predator responses in a threatened mammal

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Abstract

1. Incorporating an understanding of animal behaviour into conservation programmes can influence conservation outcomes. Exotic predators can have devastating impacts on native prey species and thwart reintroduction efforts, in part due to prey naïveté caused by an absence of co-evolution between predators and prey. Attempts have been made to improve the anti-predator behaviours of reintroduced native prey by conducting laboratory-based predator recognition training but results have been varied and have rarely led to improved survival in reintroduction programmes.

2. We investigated whether in situ predator exposure could improve anti-predator responses of a predator-naïve mammal by exposing prey populations to low densities of introduced predators under controlled conditions. We reintroduced 352 burrowing bettongs to a 26-km^2 fenced exclosure at the Arid Recovery Reserve in South Australia and exposed them to feral cats (density 0.03–0.15 cats/km^2) over an 18-month period. At the same time, we translocated a different group of bettongs into an exclosure free of introduced predators, as a control. We compared three behaviours (flight initiation distances, trap docility and behaviour at feeding trays) of cat-exposed and control bettongs before the translocations, then at 6, 12 and 18 months post-translocation.

3. Cat-exposed bettongs displayed changes in behaviour that suggested increased wariness, relative to control bettongs. At 18 months post-reintroduction, cat-exposed bettongs had greater flight initiation distances and approached feed trays more slowly than control bettongs. Cat-exposed bettongs also increased their trap docility over time.

4. *Synthesis and applications*. Translocation is recommended as a conservation tool for many threatened species yet success rates are generally low. We demonstrate that controlled levels of in situ predator exposure can increase wariness in the behaviour of naïve prey. Our findings provide support for the hypothesis that in situ predator exposure could be used as a method to improve the anti-predator responses of predator-naïve threatened species populations.

KEYWORDS
anti-predator responses, anti-predator training, burrowing bettong, exotic predator, predator exposure, prey behaviour, prey naïveté, threatened species

1 | INTRODUCTION

The application of behavioural research to conservation management is a rapidly developing field because by focussing on behavioural deficiencies or behavioural problems, managers can significantly improve conservation outcomes (Blumstein & Berger-Tal, 2015; Greggor et al., 2016). Behavioural responses influence how animals respond to a changing climate (Charmantier et al., 2008), affect the success of reintroductions of naïve species into environments with predators (Moseby et al., 2011) and are indicators of the effectiveness of conservation management strategies (Kotler, Morris, & Brown, 2007). Applications of behavioural research to conservation include the development of non-lethal mitigation strategies for European badger (*Meles meles*)–human conflict (Baker, Ellwood, Watkins, & MacDonald, 2005), and the development of taste aversion baits to reverse the decline of endangered northern quolls (*Dasyurus hallucatus*) caused by ingestion of invasive toxic cane toads (*Bufo marinus*) (O'Donnell, Webb, & Shine, 2010).

Prey naïveté is thought to be a leading cause of population decline and reintroduction failure in threatened species because prey are unable to mount effective anti-predator behaviours against introduced predators (Banks & Dickman, 2007; Cox & Lima, 2006; Van Heezik, Seddon, & Maloney, 1999). This is the result of a combination of lack of evolutionary exposure to introduced predators (Carthey & Banks, 2014; Sih et al., 2010) and/or long-term ontogenetic isolation from predators, common in species bred in captivity or maintained within fenced reserves or on predator-free islands. Prey naïveté can be expressed at three levels, whereby prey fail to recognise the predator as a threat, respond inappropriately to the predator or are simply outgunned (Banks & Dickman, 2007).

Practitioners have attempted to improve the anti-predator responses of naïve prey through training which involves simulations intended to prompt predator recognition and anti-predator behaviour (Azevedo & Young, 2006; Griffin, Blumstein, & Evans, 2000; McLean, Lundie-Jenkins, & Jarman, 1996; Miller et al., 1990; Moseby, Cameron, & Crisp, 2012). Trialled training approaches include exposing prey to pictures/models, scents or calls of predators which are paired with an unpleasant experience such as flung elastic bands, water pistols, alarm calls and simulated attacks (Maloney & McLean, 1995; Moseby et al., 2012). Although in some instances these methods have successfully improved predator recognition, few studies have shown that exposure to artificial predator stimuli has improved survival after reintroduction (but see White Jr, Collazo, and Vilella (2005)).

The low success rate in laboratory-based predator training is not surprising given the complex cues used by prey to identify predators, assess predation risk and evade predation. Prey use a variety of cues including visual recognition (Blumstein, Daniel, Griffin, & Evans, 2000), odour signals (Monclús, Rödel, Von Holst, & De Miguel, 2005), vocalisations (Blumstein, Cooley, Winternitz, & Daniel, 2008; Hettena, Munoz, & Blumstein, 2014), indirect cues such as microhabitat features (Orrock, Danielson, & Brinkerhoff, 2004) and combinations of the above (Brown & Morgan, 2015). Predator discrimination abilities are also learnt by observing the response of conspecifics to predators (Griffin & Evans, 2003) and by direct interactions with predators (Chivers & Ferrari, 2013). It is therefore unlikely that the fear elicited by an artificial unpleasant experience in the laboratory comes close to providing the same learning opportunities as those experienced by prey in the wild. However, some studies have used real predators as models to train captive-bred animals by presenting live co-evolved predators but preventing them from coming into contact. This approach has successfully improved post-release survival in Houbara bustards (*Chlamydotis undulata*; Van Heezik et al. (1999)).

Theory suggests that anti-predator behaviours can be quickly gained or lost when there is strong selection for successful anti-predator traits (Blumstein & Daniel, 2005; Strauss, Lau, & Carroll, 2006). Rapid acquisition of anti-predator behaviours has been demonstrated in impala (*Aepyceros melampus*) and wildebeest (*Connochaetes taurinus*) where vigilance behaviour increased within 3 months of the reintroduction of large felids (Hunter & Skinner, 1998) and in moose where behavioural responses to wolf howls occurred within a single generation following the reintroduction of wolves (Berger, Swenson, & Persson, 2001). Moseby, Blumstein, and Letnic (2015) proposed using in situ predator exposure to improve the anti-predator responses of naïve prey to introduced predators. In situ predator exposure involves exposing wild prey populations to controlled densities of live introduced predators in an attempt to facilitate learning and natural selection. Moseby et al. (2015) argued that many reintroduction programmes into environments with predators fail because naïve prey lack appropriate anti-predator behaviour. They suggest that exposing prey to very low densities of exotic predators may provide opportunities for animals to learn anti-predator behaviours and for improved survival traits to be selected for via natural selection. Other potential advantages of in situ predator exposure over captive-based training are that the cues used to identify predators do not need to be identified or simulated, the fear response is real and it allows for natural selection to occur by selecting for physical and behavioural traits that improve anti-predator behaviour. In situ predator exposure could also support individual learning as a result of surviving encounters with predators or through indirect cultural transfer (Ferrari & Chivers, 2008; Lucon-Xiccato, Chivers, Mitchell, & Ferrari, 2016; Smith, Arcese, & McLean, 1984). In this study, we aimed to test whether in situ predator exposure could change the anti-predator behaviour of a marsupial prey species, the burrowing bettong (*Bettongia lesueur*) which was ontogenetically naïve to predators.

2 | MATERIALS AND METHODS

2.1 | Study site and species

We studied bettongs at the Arid Recovery Reserve in South Australia. Arid Recovery is a 123-km^2 private conservation reserve, divided into six experimental exclosures surrounded by a 1.8-m high floppy top fence (Moseby & Read, 2006). The fence is designed to exclude introduced cats, foxes and rabbits (*Oryctolagus cuniculus*) and native dingoes (*Canis lupus dingo*). Rabbits, cats, foxes and dingoes have been removed from four exclosures (60 km^2). The other two exclosures

(63 km²) are used for predator manipulation studies and still contain rabbits. In this study, we used one of the four feral-free exclosures (First Expansion, 8 km²) as the control site and one of the predator manipulation exclosures (Red Lake Exclosure, 26 km²) as the treatment site. The two exclosures are within 10 km of each other so experience the same rainfall and seasonal conditions and are similar in their habitat composition, consisting of longitudinal sand dunes supporting *Acacia* and *Dodonaea* shrubland, clay interdunal swales with chenopod shrubland and mulga (*Acacia aneura*) sand plains.

Burrowing bettongs are bipedal medium-sized nocturnal marsupials (1.5 kg) that live communally in burrow systems. Bettongs were extinct from mainland Australia by the 1960s due to predation by foxes and feral cats, but persisted on some offshore islands (Short & Turner, 1993). Dingo predation (Allen & Fleming, 2012), competition with rabbits and pastoral activities have also been implicated in their decline (Short & Turner, 2000). The burrowing bettong population used in this study was ontogenetically naïve towards mammalian predators at the commencement of the study and was sourced from island populations that had been largely isolated from all mammalian predators for over 7,000 years (Lewis, Sloss, Murray-Wallace, Woodroffe, & Smithers, 2013).

Burrowing bettongs that came from island populations were reintroduced to the reserve in 1999 where they have successfully established (Moseby et al., 2011). Bettongs within Arid Recovery are protected from introduced mammalian predators by the exclusion fence but are still exposed to wedge-tailed eagles (*Aquila audax*) if they emerge during the day from their burrows. Reintroductions of burrowing bettongs to nearby areas outside the Arid Recovery Reserve have failed due to predation from predators including cats, foxes and dingoes (Bannister, Lynch, & Moseby, 2016; Moseby et al., 2011). Similarly, reintroductions of burrowing bettongs and related bettong species outside fenced reserves at other locations on mainland Australia have failed due to predation (Bellchambers, 2001; Christensen & Burrows, 1995; Priddel & Wheeler, 2004; Short, Bradshaw, Giles, Prince, & Wilson, 1992; Short, Kinnear, & Robley, 2002).

2.2 | Experimental approach

In June 2014, we trapped, marked and fitted VHF radiocollars (25 g; Sirtrack Ltd., Havelock North, New Zealand) to 40 burrowing bettongs (19 females, 21 males) in the predator-free Main Exclosure. Bettongs were trapped in Sheffield wire cage traps set at bettong warrens. Each trap had a hessian sack placed over the back half of the trap. Traps were set during the afternoon, baited with a mixture of peanut butter and rolled oats, and checked between 2 and 6 hr after dark. Radiocollared bettongs were released at point of capture. We conducted three behavioural tests on each radiocollared bettong to measure flight initiation distance (FID), trap docility and behaviour while foraging as measures of baseline anti-predator abilities before they were translocated to one of two treatments (details of the behaviour tests are outlined below).

In October 2014, radiocollared bettongs were trapped at their warrens and moved into either the cat-exposed or control treatment area.

Bettongs were randomly assigned to a treatment. Unfortunately, due to some collar issues not all collared bettongs were available for translocation. We moved 23 radiocollared bettongs (11 females, 12 males), along with 329 uncollared individuals, to the cat treatment exclosure, a 26-km² section of the reserve located 10 km north of their capture location. At the time of the translocation, the cat treatment exclosure contained no bettongs, low densities of rabbits and one feral cat. An additional five desexed feral cats (four male, one female) were added between June and August 2015 from wild individuals captured adjacent to the study site. The density of feral cats (0.19 cats per km²) in the cat-exposed area was intended to replicate the lower end of the range of feral cat densities reported in arid Australia (Legge et al. 2017).

We translocated 10 radiocollared individuals (five females, five males) to the control treatment exclosure, the feral-free First Expansion, 8 km². The control exclosure already contained bettongs, so 22 individuals were removed from one section of a dune to enable the control group to establish in unoccupied habitat. No incursions of predators to this exclosure occurred during the study period.

We compared the behaviour of bettongs that were moved into an area with feral cats "cat-exposed," with "control" bettongs that were moved to an area that was cat-free. We predicted that cat-exposed bettongs would show behavioural changes consistent with increased wariness towards predators, including increased FIDs and increased vigilance while foraging. Individual differences in temperament also have fitness consequences (Smith & Blumstein, 2008) and have been related to exploratory behaviours, habitat use and predation rates (Boon, Réale, & Boutin, 2008; Fucikova, Drent, Smits, & Van Oers, 2009; Santos et al., 2015). We therefore also expected that docility, which can be scored during trapping (see Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013) may change following exposure to predators.

2.3 | Bettong behaviour

2.3.1 | Trap docility

We scored trap behaviour of collared bettongs before translocation and 6, 12 and 18 months after translocation in both treatment groups to see if docility would change with predator exposure. During trapping we scored behaviour inside traps for all collared bettongs and any conspecifics at that warren (uncollared individuals captured consistently were included in analyses for trap docility change). We dichotomously scored whether animals moved in the trap, made noise, moved immediately from the trap into a capture bag when the door of the trap was opened and whether they moved in an agitated manner once they were secured in the bag. We summed these scores and subtracted from a total score of 4 to give a trap docility score where 0 = non-docile and 4 = docile. To ensure individual scorers were consistent in their scoring, we collectively scored non-study animals prior to each trap event. Scorers worked in pairs with no talking allowed during scoring. When approaching the trap, one observer stayed 10 m from the trap and shone a low light torch on the ground next to the back of the trap to provide illumination. The scorer recorded if the

bettong moved in the trap as they approached from 10 m to 0 m. The scorer then crouched adjacent to the side of the trap, quietly placed a trap bag over the door of the trap and then opened the door. The scorer waited 3 s before removing the hessian sack from the back of the trap. Bettongs that moved into the bag before the hessian sack was removed were scored as 1 (moved immediately from trap into capture bag). For those that remained in the trap after hessian removal, the scorer blew (standardised as short, sharp blow) through the trap onto the back of the bettong at 3-s intervals to encourage it to leave the trap. Once in the bag, the bag was tied and then held suspended for 5 s to see if the bettong bounced in the bag once secured.

2.3.2 | Flight initiation distance

Flight initiation distances were measured for each collared bettong before translocation and 6, 12 and 18 months after translocation in both treatment groups.

We allowed at least a period of 1 week after trapping before FIDs were assessed to reduce the chances that this prior experience influenced normal behaviour. Because bettongs are nocturnal, we measured FIDs using a radio receiver to locate each collared bettong at night. Scorers worked alone and used the radio signal to track each bettong. The scorer approached the bettong at a walking pace of 0.5 m/s until the animal fled and then measured the distance in metres before flight was initiated. Some bettongs always stayed just ahead of the observer (deduced from a continuing waning of the signal on approach) and were "never seen" so an FID could not be calculated accurately. However, as the maximum distance which could be seen with the spotlight was 40 m, we estimated that at a minimum, all never-seen bettongs were initiating flight at a minimum of 40 m.

2.3.3 | Foraging behaviour

We radiotracked collared bettongs to their diurnal warren and set up a food tray within 20 m of the warren. Again, we allowed at least a 1-week period after a trapping event before conducting these tests.

The food tray was a 40 L bucket dug into the ground, so it was flush with the surface and filled with sand with one cup of rolled oats mixed through. We set up a video camera trap (Bushnell) 3 m from the food bowl which recorded a 60-s video when triggered by motion. We developed an ethogram to analyse the behaviour of visiting bettongs (Table 1) and used JWatcher 1.0 (Blumstein & Daniel, 2007) to score each video. We initially aimed to score the behaviour of the collared bettong but we found that the collared bettong did not always visit the tray, thus we scored the first visit to a tray by any bettong. Not all visits were of equal length so we calculated the proportion of time in sight that each bettong was engaged in three key behaviours: slow approach to tray, foraging (foraging head down only) and vigilance while foraging (foraging head up).

2.4 | Statistical analyses

To test the effect of in situ predator exposure on trap docility and FID, we used a before–after control-impact (BACI) analysis. For each time (6 m, 12 m and 18 m), the score (trap docility) or distance (FID) was subtracted from the value recorded before translocation for each individual bettong to calculate the change in behaviour. We then fitted linear mixed effects models using package lme4 (Bates, Maechler, Bolker, & Walker, 2014) in R version 3.2.2 to examine whether individual changes in trap docility and FID varied between treatments and over time. We included fixed effects of treatment (cat/control), time (6 m, 12 m and 18 m), sex, an interaction between time and treatment, and a random effect of individual to account for the multiple observations on each bettong. Normality of model residuals was checked for each score. We used "difflsmeans" in lmerTest (Kuznetsova, Brockhoff, & Christensen, 2013) to conduct comparative post hoc tests for treatment and time with Tukey correction. A significant main effect for treatment would indicate that changes in trap docility and FID scores following reintroduction differed between treatments. A significant main effect for time would indicate that these behaviours changed over time irrespective of treatment. A significant interaction between treatment and time would indicate that the trajectory of

Key	Behaviour	Description	Grouping
a	Fast approach	Hop rapidly towards food bowl without pausing	Other
b	Bipedal sniff	Stand on back legs sniffing air	Other
c	Fighting	Aggressive interactions with another bettong	Other
d	Foraging head down	Head down and foraging	Foraging
f	Foraging head up	Head up while chewing	Vigilance
g	Slow approach	Hop slowly and tentatively towards bowl, pausing and looking up	Slow approach
o	Out of sight	Out of sight of camera	Other
q	Quad sniff	On all fours sniffing ground	Other
r	Retreat	Hop backwards from food bowl 0–5 m	Other
e	Escape	Run rapidly from food tray	Other

TABLE 1 Ethogram of behaviours for burrowing bettongs visiting food trays indicating the behaviours included in each of the three behaviour categories analysed (slow approach, foraging and vigilance)

change in trap docility and FID between the treatment groups differed over time.

For behaviour while foraging we could not conduct a BACI analysis as we were unable to identify individual bettongs in the "before" videos as bettongs subsequently moved to the cat or control treatment. Instead, we examined whether there were significant behavioural differences at 6, 12 and 18 m after translocation in each treatment. We fitted linear mixed effects models in lme4 with treatment (cat/control), time (6 m, 12 m and 18 m), and an interaction between treatment and time as fixed effects, and a random effect of warren to account for the multiple observations at the same warrens over the sessions. We fitted models for the dependent variables of proportion of time spent in slow approach (as a measure of wariness), proportion of time foraging (foraging head down) and proportion of time spent vigilant while foraging (foraging head up). Again, normality of model residuals was checked for each behaviour and "diffIsmeans" was used to examine post hoc Tukey comparisons for treatment and time.

3 | RESULTS

3.1 | Trap docility

Bettongs in both treatment and control groups showed changes in trap docility over time ($F = 9.354$, $df = 2$, $p < .001$). There was no overall difference in trap docility between the treatment and control groups ($F = 1.398$, $df = 1$, $p = .242$) and no difference in trap docility between sexes ($F = 0.079$, $df = 1$, $p = .780$). The interaction between treatment and time was not significant ($F = 1.224$, $df = 2$, $p = .302$) but inspection of the results in Figure 1 suggests that trap docility scores were increasing for cat-exposed bettongs over time (and not changing in the control group). Post hoc tests revealed trap docility for cat-exposed bettongs was significantly higher at 12 months than 6 months (estimate = 1.000, $SE = 0.227$, $p < .001$) and at 18 months in comparison to 6 months (estimate = 1.100, $SE = 0.262$, $p < .001$) but scores at 12 and 18 months did not differ significantly from each other (estimate = 0.001, $SE = 0.303$, $p = .930$) (Figure 1).

3.2 | Flight initiation distance

The FID for cat-exposed bettongs increased over time, whereas the FID for control bettongs did not change (treatment*time interaction: $F = 3.625$, $df = 2$, $p = .040$; Figure 2). There was no effect of sex on FID ($F = 0.369$, $df = 1$, $p = .550$). Post hoc comparisons showed that changes in FID differed significantly between cat and control bettongs at 12 months (estimate = 18.500, $SE = 8.277$, $p = .031$) and at 18 months (estimate = 18.200, $SE = 8.678$, $p = .042$) but not at 6 months after translocation (estimate = 0.900, $SE = 7.641$, $p = .903$) (Figure 2).

3.3 | Behaviour while foraging

Bettongs in treatment and control groups differed significantly in the proportion of time spent slowly approaching the food tray ($F = 4.053$,

$df = 1$, $p = .049$) and both groups of bettongs changed their behaviour over time ($F = 3.517$, $df = 2$, $p = .037$). Inspection of the data in Figure 3 suggests that bettongs at the control site were decreasing the time spent slowly approaching the tray over time in comparison to cat-exposed bettongs. However, there was no significant interaction between treatment and time ($F = 0.478$, $df = 2$, $p = .623$).

Bettongs did not modify the time spent foraging after exposure to feral cats with no significant effects of treatment ($F = 0.007$, $df = 1$, $p = .931$) or time ($F = 0.685$, $df = 2$, $p = .511$) or an interaction between treatment and time ($F = 0.255$, $df = 2$, $p = .776$). Similarly, bettongs did not modify the time spent vigilant while foraging (head up behaviour) after exposure to feral cats (treatment × time interaction $F = 1.791$, $df = 2$, $p = .177$; treatment $F = 0.001$, $df = 1$, $p = .982$; time $F = 0.061$, $df = 2$, $p = .941$).

4 | DISCUSSION

Using multiple lines of evidence, our study shows that in situ exposure of naïve prey to an introduced predator elicits behavioural shifts consistent with heightened wariness towards predators. Our results show that bettongs became significantly harder to approach, and there was a trend towards increased docility and increased vigilance while foraging relative to control animals after 18 months of exposure to feral cats. In the case of FID and trap behaviour, we were able to measure
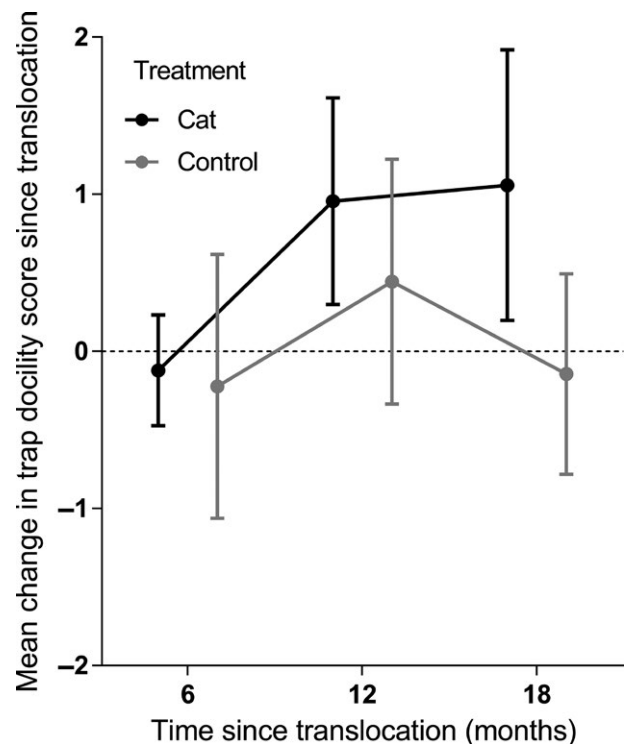
FIGURE 1 Difference in individual trap docility scores over time relative to pre-release scores for burrowing bettongs exposed to feral cats (6 m $n = 50$, 12 m $n = 23$, 18 m $n = 17$) and control bettongs (6 m $n = 9$, 12 m $n = 9$, 18 m $n = 7$). Error bars show 95% confidence intervals
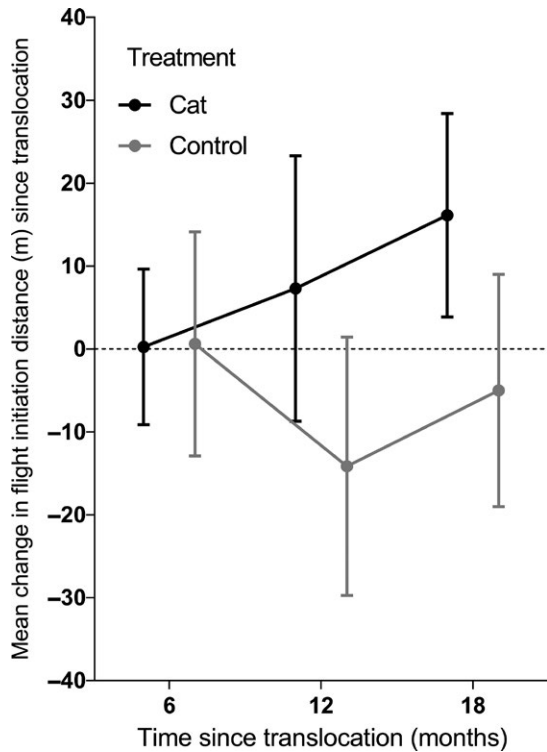
FIGURE 2 Difference in individual flight initiation distances (in metres) relative to pre-release distances for burrowing bettongs exposed to feral cats (6 m n = 16, 12 m n = 10, 18 m n = 7) in comparison to control animals (6 m n = 8, 12 m n = 7, 18 m n = 7) at 6, 12 and 18 months after translocation. Error bars show 95% confidence intervals

changes in behaviour of individual bettongs over time suggesting that the behaviour shifts we observed are the result of individual learning rather than selection.

The changes in behaviour that we observed are likely to represent an improvement in anti-predator behaviour in cat-exposed bettongs. FID is known to be a flexible anti-predator behaviour, with tammar wallabies (*Macropus eugenii*) exposed to mammalian predators having higher FIDs than their insular island counterparts (Blumstein, 2002). The rapid learning of this behaviour in our study suggests that in situ exposure can, at least to some extent, reverse the loss of these behaviours following long-term isolation from predators. FID can also be used as a measure of "boldness" (Petelle et al., 2013) with our results indicating a decrease in bold behaviour in cat-exposed bettongs relative to control. The changes in behaviour recorded by cat-exposed bettongs were consistent between individuals but confidence intervals suggested variation in the degree of change between individuals. Natural selection could strengthen population-level behavioural change over time by selecting for individuals with the fastest or greatest magnitude of change. Such selection could assist with improved survival after exposure to predators. Releases of swift foxes (*Vulpes velox*) found that bolder foxes were more likely to die after translocation because they took more risks (Bremner-Harrison, Prodohl, & Elwood, 2004) and wild-caught brushtail possums that showed most fear during handling had higher survival chances post-translocation

(Cremona, Mella, Webb, & Crowther, 2015). To our knowledge, this is the first study to test whether FID can be adjusted through training and is an important finding in the application of this technique to other species reintroductions. While we believe our method of using radiotracking and sight to collect nocturnal FIDs was reliable, we must acknowledge that this method has its limitations in comparison to diurnal studies, because the observer was unable to sight the animals until they were within 40 m. To overcome these limitations, future studies could fit collars capable of collecting fine-scale movement or proximity data to predators and prey to try to understand real-time FIDs rather than those initiated by the approach of a human.

We found a significant difference in trap docility between cat-exposed and control bettongs with a trend for increased docility in cat-exposed bettongs over time. As we did not observe the same pattern change in docility in control bettongs, it is unlikely that this was the result of habituation to trapping. Increased docility may confer a survival advantage in predator situations. Theory predicts that the optimal strategy for prey that detect a predator is to run as soon as they detect a predator approach, or hide and only flee when they have been detected by the predator (Broom & Ruxton, 2005). Bettongs that remain quiet and docile in traps may be exhibiting hiding behaviour, assessing predation risk and reducing the chance of detection. Our interpretation that the trend for increased docility in cat-exposed bettongs could be an anti-predator response is supported by studies showing that Siberian polecats (*Mustella eversmanni*) increased their hiding time after exposure to a model predator paired with an aversive stimulus (Miller et al., 1990) and Masked Bobwhites (*Colinus virginianus*) learnt to hide when exposed to dogs (*Canis familiaris*) (Ellis, Dobrott, & Goodwin, 1978).

The behavioural changes recorded in bettongs exposed to cats may have been generated through a range of pathways including observing attacks on conspecifics (Ferrari & Chivers, 2008; Lucon-Xiccato et al., 2016), personal experience (Smith et al., 1984) or filial transfer (learning from parents). Failed predation attempts are likely to provide important opportunities for learning. While the hunting behaviour of cats was not recorded in our study, we know that feral cats do not successfully kill prey during every attack and only two of the collared bettongs were confirmed as being killed by cats in this study. A reintroduction of the western quoll (*Dasyurus geoffroii*), a native marsupial of similar size to a bettong, found many quolls escaped cat predation attempts, often with horrific injuries (K. Moseby, pers. obs.). In other feline species such as lions, predation failure rates can be as high as 71% (Orsdol, 1984). Advances in video camera collars for predators (McGregor, Legge, Jones, & Johnson, 2015) may be a useful method of improving our understanding of predator–prey interactions in future studies. Understanding the interaction between learning pathways would assist in accelerating in situ anti-predator training and determining which predator and prey species should be used. Bettongs are social animals that share warrens and vocalise using a range of sounds including alarm calls and contact calls (Sander, Short, & Turner, 1997). It is likely that this may have assisted with the learning process through cultural transmission. Other studies have found learning can occur in macropods through some individuals serving as demonstrators (Griffin
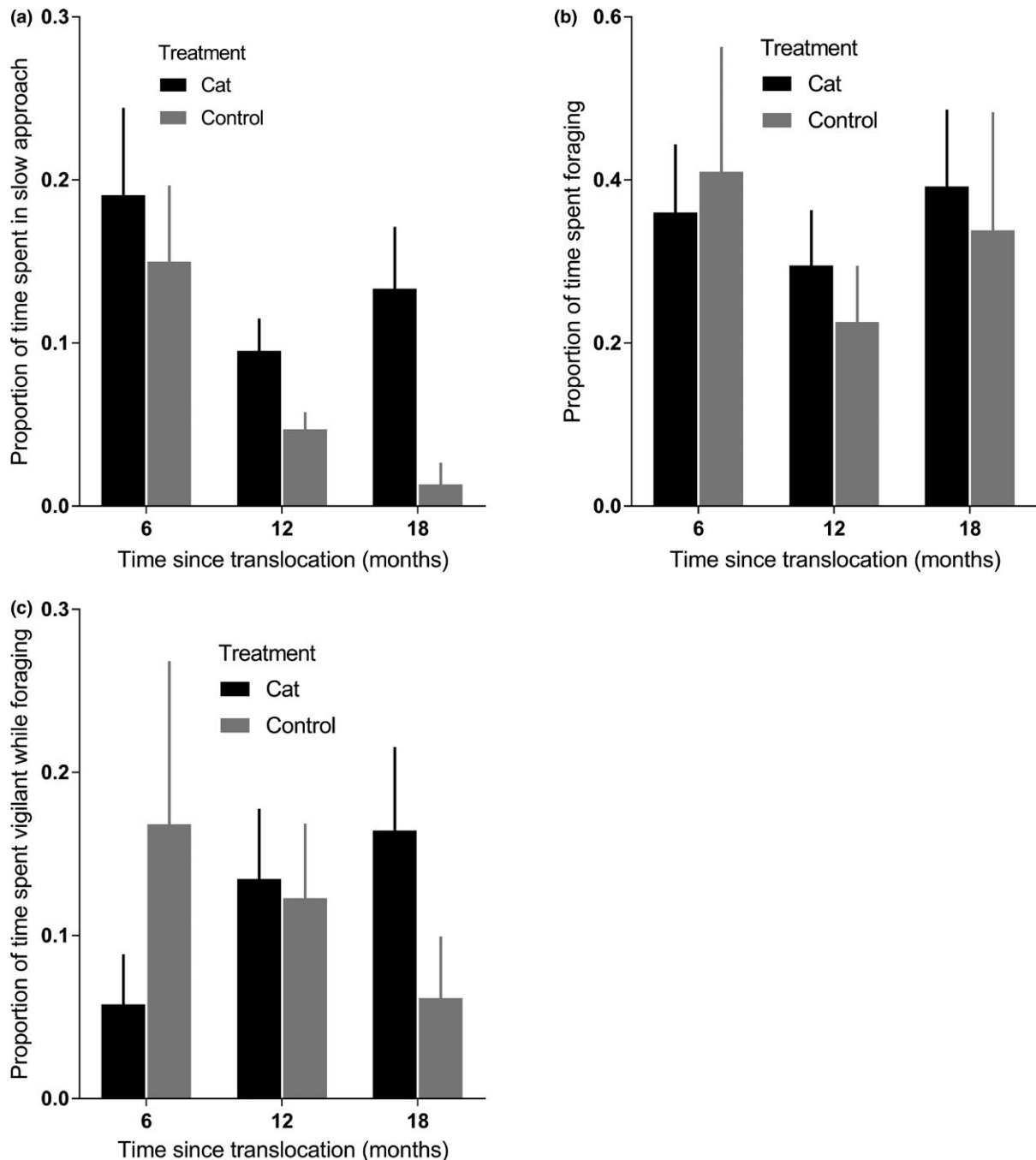
FIGURE 3 Proportion of time cat-exposed (6 m *n* = 14, 12 m *n* = 17, 18 m *n* = 9) and control burrowing bettongs (6 m *n* = 6, 12 m *n* = 7, 18 m *n* = 6) spent engaged in (a) slow approach (b) foraging (head down) and (c) vigilant behaviour while foraging (head up) at feed trays at 6, 12 and 18 months after translocation to treatment

& Evans, 2003). White-nosed coati (*Nasua narica*) also live in social groups and use vocalisations, social vigilance and keeping juveniles in the centre of the group to reduce predation rates (Hass & Valenzuela, 2002). Similarly, young bettongs stay with their mothers for many months with females sharing warrens with their mothers in adulthood, providing opportunities for filial transfer (Sander et al., 1997). The capacity of other species to learn to avoid predators under in situ predator training scenarios may be related to their social structure and length of parental care.

The critical question for our study is at what stage behavioural changes confer a survival advantage for reintroductions into the wild where exotic predators are present? Initial results suggest rapid behavioural change in FIDs but slower changes in vigilance behaviours. For example, bettong vigilance at foraging trays began diverging only after 18 months of cat exposure, too late to be statistically significant in this study. Previous studies and theory on predator–prey interactions suggest that prey species ability to respond to predators scales with the duration of their coexistence (Carthey & Banks,

2014). Thus, longer periods of in situ exposure to predators are likely to lead to greater behavioural change and should also enable selection to occur, favouring individuals who learn quickly or show the greatest change in anti-predator behaviour. However, a caveat of our study is that while we have demonstrated behavioural shifts in cat-exposed bettongs, we have not established whether these shifts confer a survival advantage. Demonstrating the benefits of in situ predator exposure and the duration of exposure required to confer a benefit will require comparing the survival of bettongs that have had varying periods of exposure to predators after reintroduction to the wild.

The results of this study have significant applications for improving the success of reintroductions into environments with introduced predators and facilitating future coexistence of native prey and introduced predators. We contend that the current trend towards isolating native prey from introduced predators through exclusion fencing or island reintroductions (Burns, Innes, & Day, 2012; Moseby et al., 2011; Young et al., 2013) is likely to exacerbate the problem of prey naivety because prey species lose their anti-predator responses when there is no selective pressure to maintain them (Moseby et al., 2015). However, we acknowledge that fenced reserves have been critical in preventing further extinctions and providing refuge and breeding sites for threatened species (Copley, 1999; Morris et al., 2015). By showing that exposing prey to exotic predators under controlled conditions can elicit changes in anti-predator behaviour in bettongs, our results support Moseby et al. (2015) who advocate for a shift in focus in threatened species management towards strategies that promote coexistence between native prey and introduced predators. Such exposure could occur through introducing low numbers of sterilised exotic predators onto island refuges and mainland sanctuaries or transferring captive-bred individuals to large exclosures in which they can be exposed to a predator. Closely monitoring the change in abundance and behaviour of prey populations following predator exposure will provide critical information on how species with different life histories respond to this training method and whether training is more or less effective at particular ages or generations in captivity. These predator-exposed populations could then be used as source populations for reintroductions rather than using naïve captive-bred populations. Exposure to novel predators may also help prey tolerate future incursions of other predator species, because exposure to one predator may be enough to retain or stimulate appropriate responses towards other predator species (Blumstein, 2006). While there is some element of risk involved with in situ predator exposure, we argue that unless we adopt novel and innovative approaches to threatened species management, the global extinction rate will continue to increase and more of our threatened species will be lost to future generations.

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AUTHORS' CONTRIBUTIONS

K.M., M.L. and D.T.B. conceived the ideas; R.W., K.M., M.L., D.T.B. designed the methodology; R.W. and K.M. collected the data; R.W. analysed the data and led the writing of the manuscript. All authors were involved in interpretation of the data, contributed critically to drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.kn21m (West, Letnic, Blumstein, & Moseby, 2017).

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