

Review



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In situ predator conditioning of naive prey prior to reintroduction

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Many translocations and introductions to recover threatened populations fail because predators kill prey soon after release; a problem exacerbated for predator-naive prey. While pre-release training has been shown to work in some situations, it is time consuming and relies on using inferred predator cues and treating small groups. We review a relatively new and very promising management tool: *in situ*, pre-release predator conditioning. Here, the goal is to allow prey in large enclosures to live with low densities of predators to accelerate selection for antipredator traits (in an evolutionary sense) or provide prey essential experience with predators that they will later encounter. We review the published results of a large-scale, controlled experiment where we have permitted burrowing bettongs (*Bettongia lesueur*) and greater bilbies (*Macrotis lagotis*) to live with low densities of feral cats (*Felis catus*), a species implicated in their widespread decline and localized extinction. We found that both species could persist with cats, suggesting that future work should define coexistence thresholds—which will require knowledge of prey behaviour as well as the structure of the ecological community. Compared to control populations, predator-naive prey exposed to cats has a suite of morphological and behavioural responses that seemingly have increased their antipredator abilities. Results suggest that predator-conditioned bilbies survive better when released into a large enclosure with an established cat population; future work will determine whether this increased survival extends to the wild.

This article is part of the theme issue ‘Linking behaviour to dynamics of populations and communities: application of novel approaches in behavioural ecology to conservation’.

1. Introduction

Many translocations and reintroductions to recover threatened populations fail soon after release, because predators kill prey before they adequately settle into their new environment [1–4]. A general problem is that we lack information on the specific behavioural traits that contribute to mortality. Considerable evidence suggests that predator-naive prey fare poorly [5]. Such naiveté may be natural, such as when a population is from a predator-free island, or artificially selected, such as when a wild population is translocated to a predator-free environment [6] to either secure it, or develop a breeding population for subsequent release. Regardless, to increase survival, we must quantitatively identify the impact of naiveté and develop methods to reverse it.

Pre-release training, where associative learning [7] is used to teach individuals about predators, has been employed in a number of situations and with a variety of taxa [8]. The idea is that the presence of a predator or, more often, a predatory cue is paired with an aversive event and animals learn to avoid the predator. Aversive stimuli may include rubber bands or water shot at mammals and birds, mammals being chased with capture nets, and fish being exposed to

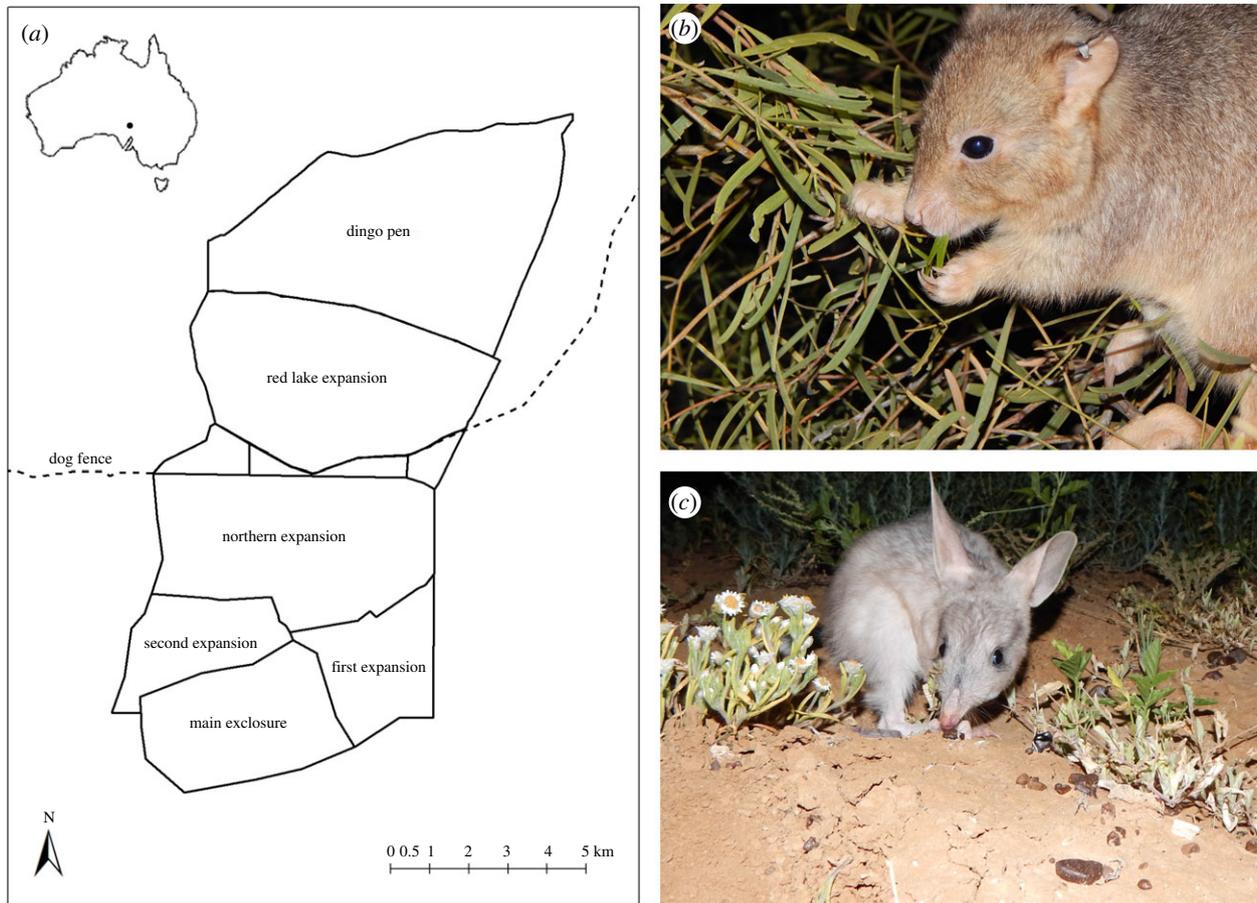


Figure 1. (a) Location of the Arid Recovery Reserve, (b) burrowing bettong, (c) greater bilby. Map modified from Moseby *et al.* [17], photos by Mike Letnic.

secretions from dead conspecifics. Fish learn especially quickly to avoid the stimulus or stimuli paired with these threats [9]. But with a few exceptions [10,11], such pre-release training in terrestrial vertebrates has not been shown to improve survival in formerly predator-naïve animals when moved to a predator-rich environment [12]. Studies that have found an improvement in survival often report only short-term survival differences after release between trained and untrained groups (e.g. [13]), which, while the first step towards developing sustainable populations, does not necessarily mean that populations will be sustainable.

We have previously proposed a novel method to prepare predator-naïve prey for subsequent translocation or reintroduction [12]. The idea is that by letting a population live with low densities of novel predators, in a sufficiently large area in which individuals can potentially escape from these predators, we can drive two processes. First, this experience may create the opportunity for prey to *learn* about their predators. By doing so, prey with some antipredator abilities may learn to associate predatory cues with the actual predators and thus learn to avoid encountering them in the future. Second, this experience could *select* for individuals that are particularly sensitive to predators or predatory cues. We expect variation in antipredator abilities and we expect variation in the ability to learn about biologically important events. Thus, we generally expect both processes to occur in nature. In addition, for social species or species that live in dense aggregations, this method may facilitate social transmission of learning [14], which may be an accelerator or force multiplier [15] because antipredator behaviour will spread through animals that are living in their natural social groups.

Regardless of the precise mechanism, *in situ* predator exposure may be a viable method by which to prepare animals before release that does not suffer from the shortcomings of staged associative learning. It also does not attempt to isolate and artificially simulate recognition based on a specific modality which may be potentially perilous because predator recognition is ultimately likely to involve multiple modalities [16]. However, as promising as the idea is, it remains to be tested. Here we review our research programme that has been evaluating the efficacy of *in situ* predator conditioning for predator-naïve greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) at the Arid Recovery Reserve in South Australia (figure 1).

2. An overview of the Arid Recovery project

The Arid Recovery Reserve (30°29' S, 136°53' E), 20 km north of Roxby Downs, South Australia, was established in 1997 and is a 12 300 ha fenced reserve [2]. The surrounding 1.8 m tall floppy-top fence was explicitly designed [18] to exclude terrestrial predators (dingoes—*Canis dingo*, European red foxes—*Vulpes vulpes*, and feral cats—*Felis catus*), but it also excludes large and introduced herbivores (red kangaroos—*Macropus rufus*, and European rabbits—*Oryctolagus cuniculus*). Australia's Dingo Fence [19] bisects the reserve and creates different densities of predators outside Arid Recovery; there are more dingoes immediately north of the fence and more red foxes south of the fence [20,21].

Located in the arid zone, rainfall is infrequent and unpredictable averaging 166 mm yr⁻¹ [22]. Arid Recovery is characterized by sand dunes separated by clay swales. Dominant plants

include sandhill wattle (*Acacia ligulata*), hopbush (*Dodonaea viscosa*), chenopods (*Atriplex vesicaria*, *Maireana astrotricha*) and mulga (*Acacia aneura*) [2].

Burrowing bettongs are a medium-sized (*ca* 1.6 kg), social, burrowing marsupial that used to range widely across over 60% of the Australian mainland [23]. Bettongs were driven extinct on the mainland following the introduction of foxes and cats and persisted only on three offshore islands [24]. They are currently listed as near threatened by the International Union for Conservation of Nature (IUCN). Greater bilbies are a medium-sized (*ca* 2.5 kg), solitary, burrowing marsupial that used to range over 70% of the Australian mainland [25]. While bilby populations were dramatically reduced by cats and foxes, they persisted in northwestern Australia [26]. They are currently listed as vulnerable by the IUCN and under the Australian Environment Protection and Biodiversity Conservation Act.

The reserve consists of six paddocks (ranging from 800 to 3700 ha), four of which are entirely free of terrestrial predators, while two presently contain cats. At the time of the research, no other large predators were introduced into the reserve, but western quolls (*Dasyurus geoffroii*) were present in two of the paddocks starting in 2015. Wedge-tailed eagles (*Aquila audax*) nest on and off the reserve and kill and scavenge on rabbits, bilbies and bettongs, and the reserve is home to a variety of elapid snakes including mulga (*Pseudechis australis*) and western brown snakes (*Pseudonaja* spp.) which are likely too small to eat adult bilbies or bettongs.

Between 1999 and 2000, greater bilbies and burrowing bettongs were introduced into the reserve's southern-most (main) paddock. Greater bilbies were introduced into Arid Recovery in 2000 and came from a captive breeding population at the Monarto Zoo [26] which originated from wild-caught bilbies from the Northern Territory and Western Australia [2]. Burrowing bettongs were originally from Bernier and Dorre Islands off the West Australian coast [24,27], and some of the bettongs originated from a predator-free enclosure on Heirisson Prong, Western Australia sourced from Bernier Island animals [2,28].

Release from predators inside the reserve has created novel management problems when bettong populations exploded (increasing from 30 to an estimated 1532 animals in one paddock in 17 years) and began to negatively impact native vegetation [29]. This surplus of otherwise endangered bettongs has created opportunities to see if they can coexist with some predators—both as a management intervention and to evaluate the idea of *in situ* conditioning.

Thus, between October and December 2014, we took 47 bilbies (27 female, 20 male) and 353 bettongs (146 female, 207 male) [30] from predator-free paddocks and moved them into the 2600 ha Red Lake paddock in which there were low densities of feral cats. It was difficult to keep cat pressure constant since cats occasionally climbed out of the paddock to leave the reserve, but, based on regular track counts, spotlight surveys and camera traps, we know that animals living there experienced between one and five cats for approximately two years [30]. We maintained a control group of both bettongs and bilbies that were captured and moved to an adjacent 800 ha predator-free paddock, and we had the remainder of animals living in other large predator-free paddocks to serve as non-manipulated controls.

We conducted a number of complementary, but not identical, studies on both species investigating how a suite of behavioural and physical traits changed over time and as a

function of predator exposure. Because of the high density of bettongs it was difficult to conduct some of the experiments on bilbies without interference from bettongs. Regardless, all of the studies aimed to quantify predator discrimination abilities as a function of predator naiveté and experience, an individual's temperament while being captured and processed, general antipredator vigilance while foraging, and flight initiation distance—as a metric of general wariness. We also made a number of morphological measurements that included body mass, pes (hind foot) length, testes width and head length, and scored animals for body condition on a 4 point scale (1 = poor, 4 = excellent) [31].

3. Key findings

We separate our key findings to date by discussing bilbies' and bettongs' knowledge of predators before release, then demonstrating, for the first time, that both populations could persist with low densities of cats, followed by discussing how behaviour and morphology changed after exposure to cats. Finally, we show that bilbies with prior exposure to cats survived longer than bilbies without any cat experience when translocated to a new paddock with cats.

(a) Predator discrimination in a predator-free environment

We conducted a number of experiments where we quantified the behaviour of predator-naive bilbies and bettongs around their burrow or at feeding trays when different predatory stimuli were present. Together, these results suggest that predator-naive bilbies and bettongs have some weak ability to detect predators; an ability that seems to scale with the evolutionary history of exposure to their predators. Thus, neither species is entirely predator naive [32–34].

Steindler *et al.* [33] quantified the emergence of bilbies from their burrows when faeces of domestic dogs, domestic cats, wild rabbits or a no-faeces procedural control were present (figure 2). We found that bilbies were more wary as they emerged from their burrows when dog faeces was present; they spent more time partially emerged from their burrow compared to other treatments. Bilbies did not respond differently when presented with cat faeces. Because dogs are related to dingoes, and because bilbies have at least 3000 years of coexistence with dingoes and less than 200 years of coexistence with cats, we concluded that this recognition ability scales with periods of coexistence.

Steindler [35] quantified bettong foraging behaviour around food mixed into the sandy substrate. A towel was attached pegged into the ground next to the food and was impregnated with whole-body scents from dingoes, cats, rabbits (a harmless control) and an unscented towel (a procedural control). A motion-sensitive game camera was triggered when an animal approached the area and we quantified the response to each scent. We found that predator-naive, burrowing bettongs were unable to discriminate between the different whole-body scents.

By contrast, predator-naive bettongs seem to have some ability to respond to the sight of predators, like other marsupials [36]. Atkins *et al.* [32] placed models of dingoes/dogs, kangaroos, red foxes and a stake (a procedural control) next to feeding stations. Again, the response of bettongs was recorded using game cameras that were triggered when an

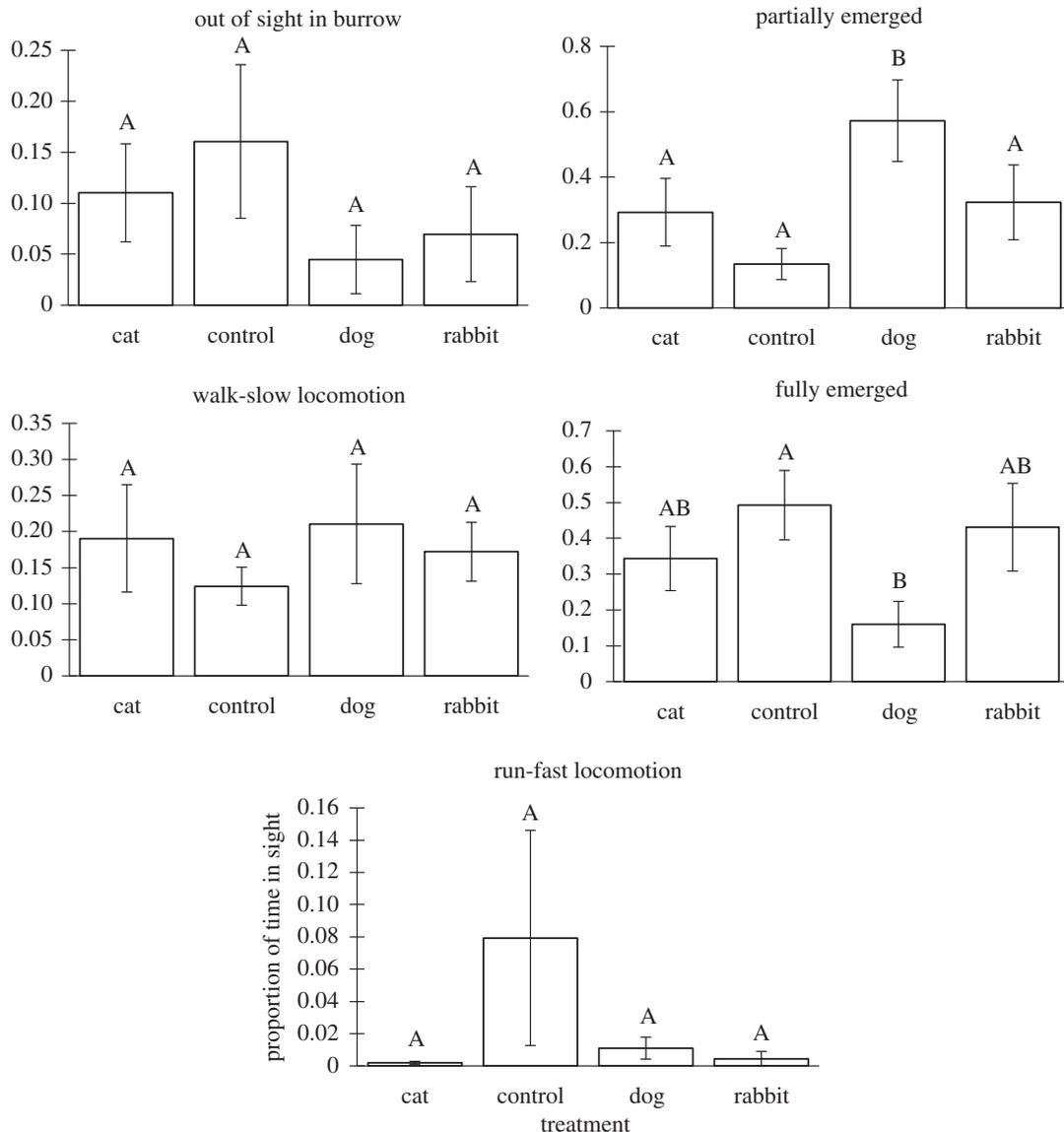


Figure 2. The response of greater bilbies when encountering faeces of domestic cats, a no-faeces procedural control, domestic dogs or wild rabbits. In all cases, time allocation (proportion of time in sight allocated to a given behaviour) is plotted on the y-axis, the treatment is plotted on the x-axis. Different letters indicate significant differences in time allocation. Modified from Steindler *et al.* [33].

individual approached the station. We found that bettongs spent slightly more time looking when at stations next to a dingo/dog model than other models. This finding is consistent with the hypothesis that bettongs had some ability to identify a predator with which they shared some evolutionary history (dingoes), but no ability to respond to the sight of a relatively novel predator (foxes). We also quantified the response of European rabbits in this experiment to our treatments and found that they had a relatively higher response to foxes—a species that they evolved with.

(b) Coexistence with cats

There was no significant difference in bettong survival following their introduction to the paddocks with cats compared to the control paddocks over the first 89 weeks following release [31].

Indeed, we found that both bettongs and bilbies can coexist with low densities of feral cats; a finding that creates a new set of questions about how one estimates coexistence thresholds. Moseby *et al.* [30] shows that populations of both bilbies and bettongs increased in the first 2 years of living with between

one and four feral cats and continued to persist when living with up to 10–12 cats. By contrast, in a previous reintroduction of bettongs, exposure to a single red fox resulted in the bettong population becoming extinct within six months. We speculate that the fox effect results from both their relatively larger body size, which means that they are able to kill larger prey, as well as their propensity to engage in surplus killing [37]. The success of the later reintroduction suggests that foxes pose more of a threat to bettongs than cats. Our results show that both bettongs and bilbies have the ability to coexist with at least one important introduced predator (cats) and future work is needed to identify coexistence thresholds [30]. Other factors that may influence such thresholds include the availability of alternative prey, predator prey preferences and hunting success, shelter type and availability, as well as a variety of environmental conditions which may influence population dynamics in the absence of predators (e.g. drought).

(c) Changes following release

By comparing the behaviour and morphology of our predator-free control subjects to our cat-exposed treatment animals, we

found that both species changed their behaviour (they became more wary around predator cues). In addition, bettongs that had been living with cats for several years had larger feet than bettongs in the predator-free area.

(i) Bilbies

Because our enclosures had many more bettongs than bilbies, we were unable to use feeding trays to study bilby behaviour due to interference from bettongs. Thus, Ross *et al.* [38] compared the latency that cat-exposed and control bilbies took to emerge from an artificial burrow within an experimental pen (without other bettongs) over a 30 min period. Control bilbies tended to emerge sooner than cat-exposed bilbies. Once emerged, we found that cat-exposed bilbies tended to spend more time in covered habitats than predator-naive bilbies in the first 5 min after release in the pen.

(ii) Bettongs

We placed towels containing the scents of potential predators—cats and Tasmanian devils (a predator species that Arid Recovery bettongs had not encountered for at least 8000 years following isolation on offshore islands), guinea pigs (a novel herbivore) and a towel soaked in deionized water (as a procedural control) next to foraging trays and used game cameras to quantify their response [39]. At the time of testing, cat-exposed bettongs had been living with cats for 24 months. We found that predator-naive bettongs did not respond differently when approaching feed trays containing the different scents. However, bettongs with 2 years of *in situ* exposure to cats approached trays with predator scents more slowly and more cautiously. Importantly, these bettongs did not discriminate between cats and Tasmanian devils. This finding suggests that exposure to some predators may trigger responses to other predators—including those which they have had no exposure to for the past 8000 years. *In situ* cat exposure may inculcate bettongs to more than simply cats. However, this finding needs follow up studies for confirmation and to better understand the scope of such predator generalization.

We placed taxidermic mounts of cats and rabbits, a plastic bucket (a novel object) and no object (as a control) next to foraging trays and asked whether bettongs exposed to cats for 8–15 months responded differently than cat-naive bettongs [34]. We found that cat-exposed bettongs spent more time cautiously approaching the cat models while control bettongs did not discriminate between models. This suggests that *in situ* exposure to cats was an experience that trained bettongs to be wary around cats.

Bettongs not only had improved predator disclination abilities; other putative antipredator behaviours also changed as a function of *in situ* cat exposure. West *et al.* [40] compared flight initiation distance, trap docility and behaviour at unmanipulated foraging trays before release, and then at 6, 12 and 18 months following release. We found that by 18 months post-release, cat-exposed bettongs had greater flight initiation distances (FID) and approached feed trays more slowly than our control bettongs (figure 3). We also found that cat-exposed bettongs became more docile in traps over time, possibly in an attempt to hide when approached by a threat. Thus, a suite of behaviours that may be involved in successful antipredator behaviour (FID, cautious eating and not overreacting to a potentially stressful situation) all are modified following experience of living with cats.

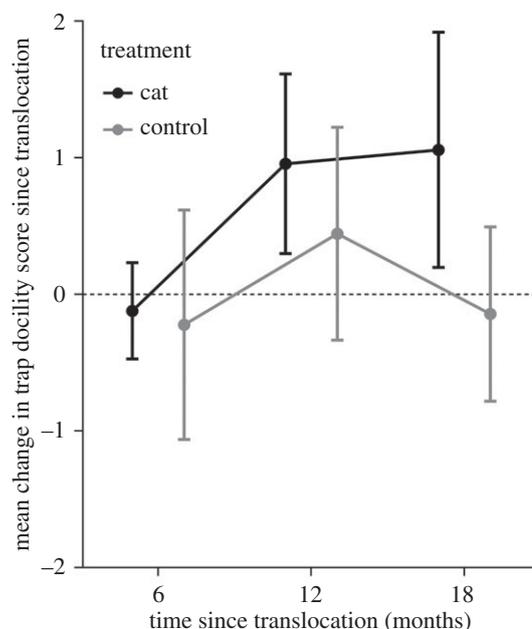


Figure 3. The change in average (\pm 95% C.I.) flight initiation distance over time since bettong release as a function of treatment (exposure to cats or control). Modified from West *et al.* [40].

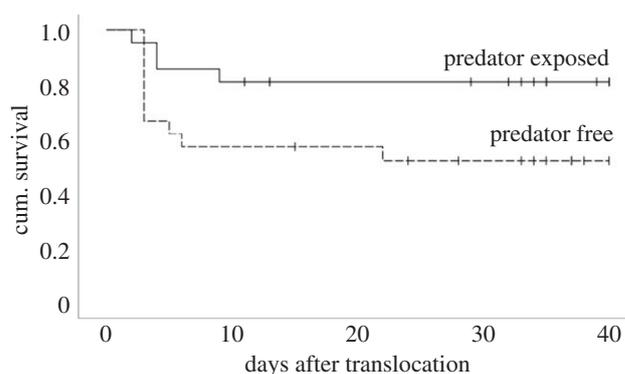


Figure 4. Bilby survival over time as a function of prior exposure to predators. Modified from Ross *et al.* [38].

Finally, we found that bettongs exposed to cats had larger hind feet than control bettongs [31]. This pattern of larger feet held both for older animals that were translocated as well as for those born into the *in situ* treatment. This suggests that predation may drive phenotypic changes. Interestingly, pes length did not explain significant variation in whether or not bettongs survived when initially translocated to the cat treatment but low mortality immediately after release may have masked any selection for physical traits [41].

(d) Increased bilby survival

To provide a test of whether *in situ* predation can enhance reintroduction success, we introduced 24 predator-naive and 23 cat-exposed bilbies into a 37 km² enclosure where 10 cats were present. This experiment [38] has shown that bilbies living with a modest density of cats (5 cats/26 km²) for 2 years survived significantly longer than predator-naive bilbies (figure 4). The first week following release was a period of high mortality, but ultimately we found that cat-exposed bilbies were significantly more likely to survive to 40 days in the new enclosure. The initial week of vulnerability

followed by essentially no further predation for the bilbies with prior exposure to predators suggests that a soft release, whereby animals were slowly acclimated or guarded in their first days following release, might be an effective strategy to enhance survival. In addition, cat-exposed bilbies were more likely to share burrows than control bilbies, a finding which suggests that these modestly social animals may engage in a social antipredator behaviour following experience with predators. The survival difference is important because the immediate period following release is the critical time for survival of reintroduced animals. Thus, *in situ* exposure to predators significantly increased immediate survival.

4. Conclusion and future research

We have shown that two species, that were either driven extinct by feral cats and foxes (mainland bettongs) or had their populations drastically reduced by cats and foxes (greater bilbies), have some latent predator discrimination abilities that seem to scale with exposure to predator experience (canids are more likely to be recognized than felids—see also [42]). In addition, we have shown that *in situ* exposure to low densities of feral cats leads to a cascade of behavioural and physical changes that seemingly prepare animals for life with predators. These traits are likely to have profound demographic consequences and were only possible because of our quantitative assessment of them. Finally, we have found that more cat-exposed bilbies survived the first 40 days following release into a cat-occupied area compared with control bilbies. Together, these results illustrate the power of using behavioural ecology theory and studies in quantitative assessments of demographic factors that influence population persistence.

Carthey & Blumstein [5] developed an eco-evolutionary framework to understand how isolation from predators may influence antipredator behaviour and prey naiveté. From this perspective, both bettongs and bilbies now face novel, exotic felid and canid predators, but because of prior exposure to dingoes, we have shown that bettongs have some ability to respond to cues from another canid. This suggests that canids share some archetype (despite quantifiable differences in olfactory profiles of dingoes and dogs—[43]). But perhaps more importantly, both species seem to be able to respond differently to cats—a truly novel predator which neither species had experience with—after a few years of living with cats. This is notable. For instance, while elk (*Cervus elaphus*) can learn quickly to respond appropriately to reintroduced wolves (*Canis lupus*) in Yellowstone, they evolved with wolves and lived in an otherwise predator-rich community [44]. Thus, from the perspective of the Carthey and Blumstein framework, both species seemingly have the ability for rapid changes in their cue discrimination abilities, which in theory portends well for living with potential novel predators.

We need to know much more about whether animals are predisposed to learn more about their predators in certain modalities and how relaxed selection may differentially work on these different modalities. For instance, a specific modality may be differentially important for nocturnal versus diurnal species as well. One might assume that nocturnal species will rely more on olfactory cues than visual cues but prior work has shown that some nocturnally active marsupials rely on visual cues [36] and seemingly

feel more secure on moon-lit nights where they have a better ability to detect predators visually [44].

Given the ability to discriminate novel predators from various controls, the question of coexistence hinges on the ability of naive prey to develop an effective antipredator response. If prey species have some ability to respond to predators, we expect that they will be able to coexist with their predators. The fact that so many reintroductions have failed when predator-naive individuals have previously been released (e.g. [37]), suggests that we might not expect that either bilbies or bettongs has an effective response. However, if responses are effective, there is hope for longer-term coexistence outside the constraints of a fenced reserve. The challenge of creating appropriate behavioural responses *de novo* is non-trivial if the animals do not have it within their capacity to marshal one. Our current results with bilbies are hopeful in this regard. If, however, there are too many predators, on-going predator management may be required even if prey have some degree of predator awareness.

Future planned studies include determining bettong survival as a function of prior *in situ* predator exposure, and determining whether survival is enhanced outside the fence in areas where predator control has reduced predator density but not eliminated predators. In addition, key remaining questions involve better understanding the coexistence thresholds with cats, whether exposure to cats inoculates bilbies against other predators such as dingoes (and potentially foxes), and whether these responses reflect plasticity or are heritable.

Taken together our work illustrates the potential benefits of *in situ* predator exposure as a method to prepare predator-naive animals for life with predators. This method may not be suitable for all threatened or endangered species and we are fortunate to have large populations to work with. But our situation is not really that unique. When prey populations have crashed because of the introduction of novel predators, a too-common occurrence on islands throughout the World as well as in Australia, removing the cause of decline (i.e. the predators) immediately solves the problem. Depending upon whether the removal is achieved in a fenced enclosure or by eradicating predators outside the fence, will determine how many situations there will be where there are a lot of animals. In Australia, there are many safe and growing populations of threatened species on islands and in fenced reserves that can be used for similar studies.

For suitable species, we hope that others will study the efficacy of *in situ* predator conditioning. Importantly, however, it is essential to compare this method to more traditional pre-release predator training. Such comparative effectiveness evaluation [45] is underused in conservation behaviour yet is essential. Importantly, future studies should compare the costs of different techniques in terms of the infrastructure and personnel required. We may have developed a novel and cost-effective method to allow vulnerable prey to gradually learn to coexist with the predators that were previously responsible for their demise.

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Authors' contributions. All authors conceived and wrote the article.

Competing interests. We have no competing interests.

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