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Individual traits influence survival of a reintroduced marsupial only at low predator densities

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Abstract

Predation is a key factor contributing to the failure of reintroductions of vertebrates but there is variation in predation risk between individuals. Understanding the traits that render some animals less susceptible to predation, and selecting for these traits, may help improve reintroduction success. Here, we test whether prior exposure to predators or specific morphological and/or behavioural attributes explained variation in post-reintroduction survival in a moderate and low predator density environment. We exposed a population of the threatened burrowing bettong (*Bettongia lesueur*) to controlled densities of feral cats (*Felis catus*) for ≥3 years. We then conducted two translocations of cat-exposed and control populations that had no exposure to predators to a new site where cats were present at moderate, then low density. Variation in survival of burrowing bettongs was not explained by prior predator exposure to predators or measured individual traits at moderate cat density. At lower cat densities, males died sooner and burrowing bettongs with larger hind feet survived longer. Although prior cat-exposure did not confer a survival advantage at low cat densities, the cat-exposed burrowing bettong population had larger hind feet (n = 44) compared to the control population (n = 45) suggesting that trait divergence between cat-exposed and non-cat-exposed burrowing bettongs may not yet be sufficient for improved survival. Alternatively, prior predator exposure may not confer a survival advantage because they are "outgunned" by evolutionarily novel cats. Predation is a major problem thwarting successful reintroductions world-wide. Exposing populations to predators over longer time periods and periodically testing survival will be required to determine whether pre-release predator exposure prepares animals for life with novel predators. Our study highlights the importance of reducing predator activity at release sites prior to reintroduction to enable any benefits from intraspecific variation in survival traits to be realised.

Introduction

Many conservation translocations and reintroductions fail (Short 2009; Wolf et al. 1996) and it is essential to understand why. Intraspecific variation in survival after reintroduction has been attributed to a variety of factors including body mass (Hamilton et al. 2010), boldness (Bremner-Harrison et al. 2004), prior exposure to predators (Ross et al. 2019) and social groupings (Shier 2006). In many cases, predation is the primary reason for reintroduction failure. Controlling or excluding introduced predators is usually a pre-requisite for reintroduction success where introduced predators are present (Fischer and Lindenmayer 2000; Moseby et al. 2011; Short 2009). This is particularly evident in Australia, where even native predators are susceptible to predation by introduced predators (Moseby et al. 2015; Radford et al. 2018). Introduced predators are thought to have a greater impact on native species than native predators because of the absence of a shared evolutionary history (Saul and Jeschke 2015). Traits that improve an individual's ability to avoid or deter predators in the initial post-release period may therefore lead to increased survival. Studies have shown that predation risk can vary between individuals of the same species based on body mass (MacLeod et al. 2006), age (Wright et al. 2006), personality (Bremner-Harrison et al. 2004) and sex (Fitzgibbon 1990). Prey facing novel predators typically have low post-release survival (Moseby et al. 2011; Short 2009), most likely due to prey naivety caused by evolutionary or ontogenetic isolation from predators (Banks and Dickman 2007; Carthey and Blumstein 2018).

With introduced predators unlikely to be eradicated from Australia in the foreseeable future, developing strategies to permit native species to co-exist with them will lead to improved reintroduction outcomes. One potential way to improve reintroduced animals' prospects of survival post-release in areas where introduced predators remain present (but subject to control) is to provide them with anti-predator training prior to release. Such pre-release training generally occurs in captivity and typically involves exposure to predators or their cues coupled with an unpleasant experience (Griffin et al. 2000; van Heezik et al. 1999; McLean et al. 1996). Whilst some studies have reported shifts in the behaviour of individuals subject to anti-predator training (Hölzer et al., 1995; Miller et al. 1990), in many cases post-release survival was not measured or improved (McLean et al. 2000; Moseby et al. 2012). This could be because the training used simulations or indirect cues, which may not induce learning of behavioural traits required to avoid or escape real predators, or because post-release survival of captive-reared animals is generally lower than for wild-to-wild translocations (Griffith et al. 1989).

An alternative way to provide animals with anti-predator training prior to reintroduction is *in situ* predator exposure, whereby populations of naïve prey are exposed to novel predators under real-life conditions prior to reintroduction (Moseby et al. 2016). The rationale behind this approach is that encounters with predators will prompt learning and selection for traits that enhance individuals' capacity to avoid fatal encounters with predators (Moseby et al. 2016). *In situ* predator exposure has been trialled at the Arid Recovery Reserve in South Australia (Blumstein et al. 2019; Moseby et al. 2018; West et al. 2018b). Populations of endangered marsupials (greater bilbies —*Macrotis lagotis*, and burrowing bettongs—*Bettongia lesueur*) have been established in a large (26 km^2) paddock with feral cats (*Felis catus*). In support of the *in situ* predation concept, a release of cat-exposed and cat-naïve bilbies found that cat-exposed bilbies had significantly enhanced short-term survival after reintroduction into an environment where cats were present (Ross et al. 2019).

Here we extend our knowledge of the factors influencing mortality from predation after release by testing the relative contribution of individual attributes and the efficacy of pre-release exposure to predators by comparing the survival of cat-exposed and cat-naïve populations following translocation to an area that contained feral cats. Previous research showed that bettongs exposed to cats in large, fenced, exclosures for several years were more wary than cat-naïve bettongs (Saxon-Mills et al. 2018; West et al. 2018b) and had longer hind feet (Moseby et al. 2018). Because these traits might be expected to influence bettongs' ability to avoid or escape predation by cats, they may also improve post-release survival of reintroduced bettongs. Furthermore, one previous study showed that post-reintroduction success of burrowing bettongs is related to movement patterns, with bettongs that forage closer to their warrens exhibiting increased survival than more wide-ranging individuals (West et al. 2018a). Building on this knowledge, we hypothesised that individuals exposed to cats prior to release would show improved survival compared to control animals, and that in particular animals with larger feet and those that used fewer warrens post release (a metric of movement) would survive longer than other individuals. The results of this study provide insights into co-existence thresholds for threatened mammals.

Materials and methods

Study species

Burrowing bettongs (hereafter 'bettongs') are bipedal, nocturnal marsupials that live communally in burrows (Sander et al. 1997). Once widespread across Australia, they became extinct on mainland Australia in the 20th century, but persisted on three feral predator-free islands in Western Australia. Bettongs have since been successfully reintroduced to cat- and fox-free fenced sanctuaries on mainland Australia (Moseby et al. 2011; Short and Turner 2000). Bettongs are considered to be highly susceptible to predation by introduced predators such as cats and foxes (*Vulpes vulpes*; Radford et al. 2018) and attempts to release them into areas with predators on mainland Australia have failed due to cat predation (Christensen and Burrows 1995) or a combination of cat, fox and dingo (*Canis lupus dingo*) predation (Bannister et al. 2016; Moseby et al. 2011).

Study site

We studied bettongs in the Arid Recovery Reserve (30°29'S, 136°53'E), a private conservation reserve situated approximately 20 km north of Roxby Downs, in arid South Australia. Average annual rainfall is 148 mm (www.bom.gov.au). Habitat consists of dunes dominated by *Acacia ligulata*, *Dodonaea viscosa* and *Zygochloa paradoxa*, interspersed with swales of predominantly *Maireana astrotricha* and *Atriplex vesicaria*, with some *Acacia aneura*. The 123 km^2 reserve is surrounded by a 1.8 m floppy-top fence (Moseby and Read 2006) and is divided into six paddocks (exclosures) (Fig. 1), four of which are free of introduced mammalian predators (feral cats, foxes and dingoes) and rabbits (*Oryctolagus cuniculus*), an introduced herbivore. Feral cats and rabbits, but not foxes or dingoes, are present in the 'Predator Paddock' (24 km^2) and the 'Release Paddock' (37 km^2, Fig. 1). We also used bettongs living in two of the 'Cat-Free Paddocks' ('First Expansion' 8 km^2 and 'Main Exclosure' 14 km^2). The experiment involved releasing bettongs from the Cat-Free Paddocks and Predator Paddock into the Release Paddock.

Predator treatments and monitoring

To obtain a population of cat-exposed bettongs, bettongs were originally reintroduced to the Predator Paddock in October 2014 from Cat-Free Paddocks (Fig. 2). Cats were removed beforehand but after a settling period were gradually added back in, where they were to co-exist with bettongs—detailed methods are given by West et al. (2018b). Cats were known to subsequently interact with or predate on bettongs (Moseby et al. 2019, K. Moseby unpub. data). In the current study, cat-exposed and cat-naïve (control)

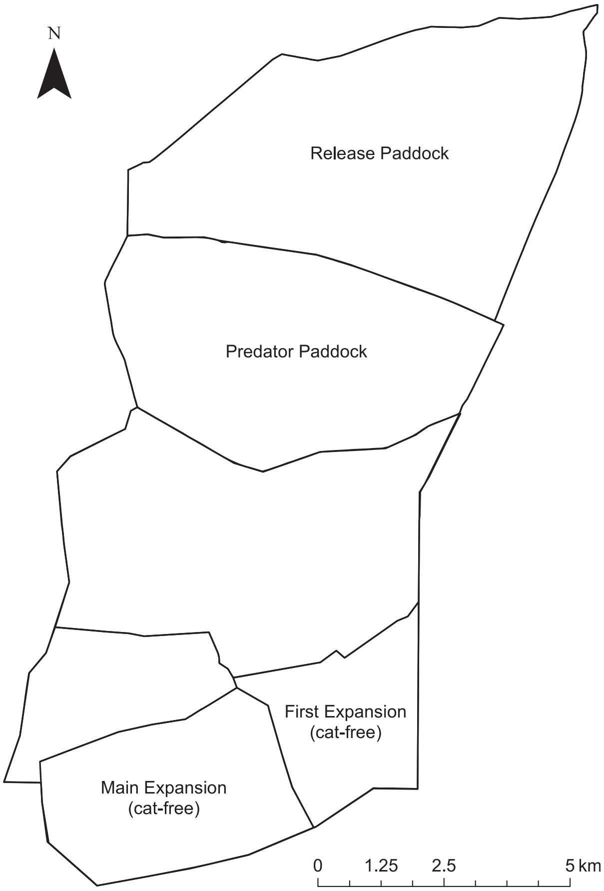

Figure 1 Arid Recovery Reserve, divided into six separate paddocks of 8–37 km^2. The four paddocks relevant to this study are named.

bettongs were translocated to the Release Paddock for two releases, in November 2017 (Release One) and November 2018 (Release Two). Cat-naïve bettongs were sourced from the First Expansion (2017) or Main Exclosure (2018) and cat-exposed bettongs were sourced from the Predator Paddock after ≥3 years of cat exposure (ca. ≤4 generations). In addition to cats, rabbits were present in both the Predator Paddock and Release Paddock. Rabbits and small mammals are regularly consumed by feral cats (Read and Bowen 2001) and thus represent alternative prey for cats than bettongs. Feral cat, bettong, rabbit and small mammal activity was monitored in the Release Paddock using remote cameras and monthly track counts. An array of 20 remote cameras (Bushnell Trophy Cam HD Aggressor) was established in September 2017. Detections at least 10 minutes apart were considered independent. Photos were not clear enough to be able to reliably identify individual cats. In October 2017, we established three 1 km track transects along dunes (see Moseby et al. (2011) for methods) and counted tracks of bettongs, cats, rabbits and small mammals. Camera and track monitoring also occurred in the Predator Paddock, and track monitoring occurred in Cat-Free Paddocks.

Release one

In August 2017, 39 bettongs weighing >1200 g from the Cat-Free Paddock (8F, 12M) or the Predator Paddock (9F, 10M) were fitted with VHF radio-collars (brass band 25 g, Sirtrack, Havelock North, New Zealand). Three months later, in November 2017, these bettongs were translocated to the Release Paddock (Table 1), where the cat density was estimated to be 0.41/km^2—within the 95% confidence interval for the average density of cats in Australia in an average year (0.18–0.45/km^2 (Legge et al. 2017)). One uncollared female from the Predator Paddock was also translocated. Cat density was estimated using a combination of remote camera detections combined with subsequent removal of cats. None of the radio-collared bettongs from the Predator Paddock (cats present) died during the three months prior to translocation. Bettongs were captured in treadle-operated cage traps baited with peanut butter and rolled oat balls, following standard operating procedures (Petit and Waudby 2012). Captured bettongs were weighed and had hind foot (*pes*) length, head length and testes width/pouch status recorded (Table 2). Body measurements were taken to the nearest 0.1 mm using steel callipers. Each bettong was given a uniquely numbered ear tag. Bettongs were either released directly into rabbit warrens (in pairs) in the Release Paddock if released in the early morning, or were released near rabbit warrens if released in the evening. Where possible, for releases into warrens, two bettongs from one source (1M, 1F, where possible) were released into a single warren, with two bettongs from the opposite source released into an adjacent warren (≤100 m away). Two of the females had small pouch young at the time of translocation.

Release two

Once radio-collars were removed from the remaining four bettongs in the Release Paddock after Release One, no tracks were detected two months later and no bettongs were seen on remote camera six months later—presumably they died either from natural causes or, more likely, from cat predation. We therefore elected to reduce the number of cats in the Release Paddock to a point where the camera detection rates were less than half that recorded at the time of the first release. Six cats (5 adults, 1 juvenile) were removed while bettongs from Release One persisted (adaptive management in response to high bettong mortality rates), and another 6 adult cats were removed after bettong activity ceased in the Release Paddock, leaving an estimated density of 0.11/km^2 (cats were identified on camera and/or when later removed, estimating four cats remaining for Release Two). Following cat control, in November 2018 we again translocated bettongs from the Predator Paddock and a Cat-free Paddock to the Release Paddock (Table 1). Twenty from each source (10F, 10M) were fitted with VHF collars and another five females from each source were fitted with GPS collars (Litetrack 30, 35 g, Sirtrack Havelock North, New Zealand) at the time of release. No females had pouch young. Bettongs were released at two release sites either at night or into

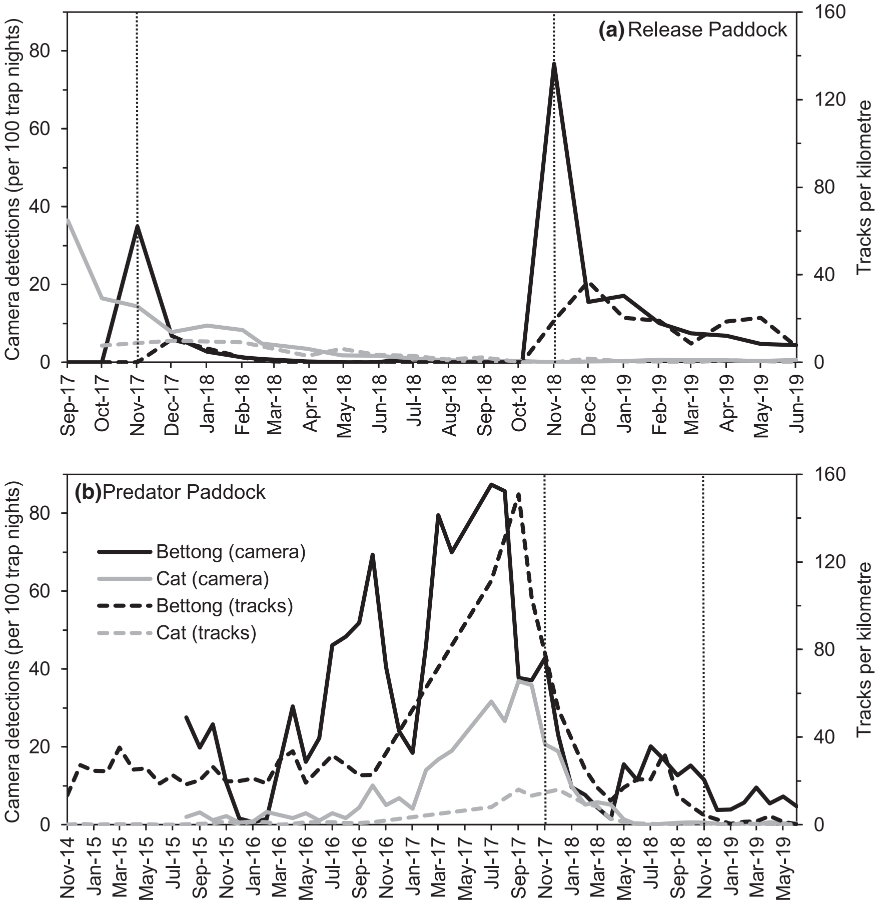

Figure 2 Burrowing bettong and feral cat activity in the Release Paddock (a) and Predator Paddock (b) monitored by remote camera and track counts (secondary y-axis). Vertical lines represent bettong releases in the Release Paddock, and removals in the Predator Paddock. A large number of cats (>40) were deliberately removed from the Predator Paddock in January 2018 (Moseby et al. 2020).

warrens in the morning (as per Release One), with half from each source at each.

Monitoring

Bettongs were radio-tracked to their warrens, where possible, twice in the first week after release and weekly thereafter. If a collar emitted a mortality signal, the individual was tracked to its location where we took photographs, recorded evidence of predation and collected DNA swabs of the collar and/or carcass. Swabs were sent to Helix Molecular Solutions (Crawley, Western Australia) for predator species identification; detailed methods are given by Moseby et al. (2015). Bettongs that survived the monitoring period were captured and their collars were removed.

Data analysis

A multivariate analysis of variance (MANOVA) was used to compare physical traits (body mass, hind foot length, head length and body condition index [(weight$^{1/3}$)/hind foot length] of released animals by sex, release year and treatment (including interactions). Assumptions of normality were met. Survival analysis was conducted separately for each release because of dramatically different survival periods for the two releases, the difference in cat activity recorded during each release, and differences in physical traits between release years. We analysed survival in both experiments by fitting a Cox Proportional Hazards regression (Cox 1972) to investigate how treatment as well as sex, hind foot length, head length and, for Release Two in 2018, the proportion of unique warrens used (number of unique warrens used divided by number of times radio-tracked to a warren) influenced survival. Proportion of unique warrens used was not included in the analysis of Release One because many animals were killed soon after release, skewing the data. The Cox Proportional Hazards regression allows for censored data and the hazard function produces a conditional likelihood providing inferences about the unknown regression coefficients (Cox 1972). We calculated correlation coefficients prior to analysis to screen for multicollinearity (correlation values were <0.3). We verified assumptions of the model by checking Rho values; none were significant.

Table 1 Burrowing bettong translocations

Release	Year	Cat exposed	No. translocated	Bettong activity at source (tracks/km)	Cat activity at source (tracks/km)	Cat activity at release site (tracks/km)
One	2017	Yes	20 (10F, 10M)	122 ± 15	13.3	7.6
One	2017	No	20 (8F, 12M)	245 ± 56	0	7.6
Two	2018	Yes	25 (15F, 10M)	19 ± 3	0.3	0*
Two	2018	No	25 (15F, 10M)	149 ± 58	0	0*

Bettong activity at each source was averaged over the 6 months prior to translocation. Cat activity was recorded in the month prior to translocation.

*Despite cat activity (tracks/km) being 0 prior to release, cats were known to be present based on remote camera data.

Results

Although there were no significant differences in traits between the cat exposed and cat naive bettongs in 2014 when they were initially separated into two treatment groups, cat-exposed bettongs gradually changed over time with cat exposure (Moseby et al. 2018). At the start of the present experiment in 2017 there were significant differences in physical traits; on average, cat-exposed bettongs were significantly heavier, had longer feet, longer heads and better body condition than cat-naïve bettongs (Tables 2 and 3). In addition to differences between treatments, bettongs in Release One were significantly heavier, had longer heads and better body condition than bettongs in Release Two. On average, male bettongs were heavier and had better body condition than female bettongs.

In the month prior to Release One, cat activity on transects was 7.6 tracks/km (camera detections 16.4/100 trap nights). Cat activity was reduced to 0 on track counts (camera detections 0.3/100 trap nights) prior to Release Two (Fig. 2). Rabbit activity in the Release Paddock was more than twice as high during the first release (136 tracks/km) compared to the second release (55 tracks/km), while small mammal activity fluctuated throughout.

Survival (to collar removal) for both releases was ultimately poor with 27.9 % of cat-exposed bettongs and 25 % of cat-naïve bettongs surviving to collar removal, but over different time periods. In Release One, 15.8 % of cat-exposed bettongs (3 of 19) and 5.0 % of cat-naïve bettongs (1 of 20) survived to collar removal around 100 days after release [Kaplan Meier probability of survival at day 100 = 0.10 (95% CI 0.03–0.22)]. Collars were removed at this stage because we felt the cost and logistic effort required to monitor a such small number of animals (4) over a longer period was not of benefit considering the remote nature of the field site. Cats were confirmed killers of 88 % of dead radio-collared bettongs based on DNA results, even when wedge-tailed eagles had interfered with carcasses. Because no DNA was able to be extracted from the remaining swabs, cause of death remained unclear. In Release Two, 37.5 % (9 of 24) of cat-exposed bettongs and 41.7 % of cat-naïve bettongs (10 of 24) survived to collar removal around 250 days after release (Table 4), with a 0.96 probability of survival to day 100 (95% CI 0.84–0.99). The probability of survival to 100 days for bettongs released at low cat density (Release Two) was higher (0.96) than at moderate cat density (0.10) (Release One). When the two releases were pooled, there was no difference in the probability of survival to day 100 based on treatment, with a probability of 0.58 (95% CI 0.43–0.73) for cat-exposed bettongs, and a probability of 0.55 (95% CI 0.39–0.68) for cat-naïve bettongs.

Patterns of decline differed between the two releases; during Release One, survival rapidly declined following the release. For Release Two, post-release survival was much higher until 200 days post-release, when there was a rapid decline in survival (Fig. 3).

No significant variation in survival duration was explained by our measured variables for Release One (Table 5). By contrast, in Release Two, we found that having a large hind foot decreased the risk of mortality and there were trends towards males dying sooner than females, and those with smaller heads surviving longer (Table 5).

Discussion

Despite the experimental burrowing bettong population being exposed to feral cats for at least three years, prior exposure to this predator did not confer a survival advantage to

Table 2 Physical traits for bettongs at the time of release (mean ± 1SE). BCI = body condition index ((body mass$^{1/3}$)/hind foot length)

	2017 Cat-exposed		2017 Cat-naïve		2018 Cat-exposed		2018 Cat-naïve	
	Female	Male	Female	Male	Female	Male	Female	Male
No. released	10	10	8	12	15	10	15	10
Body mass (g)	1554 ± 36	1777 ± 28	1444 ± 56	1642 ± 42	1558 ± 35	1711 ± 54	1428 ± 33	1398 ± 51
Hind foot length (mm)	105.4 ± 0.5	106.6 ± 1.1	103.9 ± 1.6	104.4 ± 1.0	104.6 ± 0.7	105.3 ± 0.9	102.6 ± 0.6	103.9 ± 0.7
Head length (mm)	77.8 ± 0.8	78.4 ± 0.8	76.6 ± 0.7	76.7 ± 0.9	80.7 ± 0.8	81.3 ± 0.5	77.2 ± 0.6	78.5 ± 0.7
BCI	4.91 ± 0.10	5.56 ± 0.07	4.63 ± 0.16	5.24 ± 0.11	4.96 ± 0.10	5.42 ± 0.16	4.64 ± 0.09	4.48 ± 0.15

Table 3 Results of a MANOVA, investigating pre-existing differences in body mass, hind foot length, head length and body condition index (BCI) for burrowing bettongs by release year, treatment (cat-exposed and cat-naïve), sex, release year × sex and release year × treatment

Dependent variable	Factor	*F*-value	df	*P*-value
Body mass	Release year	11.9	1	0.0009*
	Sex	14.7	1	0.0002*
	Treatment	29.3	1	<0.0001*
	Release year × treatment	1.8	1	0.19
	Release year × sex	6.6	1	0.012*
Hind foot length	Release year	3.3	1	0.072
	Sex	1.5	1	0.23
	Treatment	8.4	1	0.0048*
	Release year × treatment	0.03	1	0.87
	Release year × sex	0.005	1	0.95
Head length	Release year	13.6	1	0.0004*
	Sex	1.3	1	0.26
	Treatment	21.5	1	<0.0001*
	Release year × treatment	2.6	1	0.11
	Release year × sex	0.3	1	0.59
BCI	Release year	10.1	1	0.0021*
	Sex	14.4	1	0.0003*
	Treatment	25.1	1	<0.0001*
	Release year × treatment	2.5	1	0.12
	Release year × sex	7.9	1	0.0062*

Measurements were taken at the time of translocation.
*Indicates significance ($P < 0.05$).

bettongs at moderate or low cat densities. A lower cat density permitted a longer survival time for both treatments, but even the lower cat density of 0.11/km^2 was too high to permit co-existence of a newly reintroduced population, with the population ultimately declining prior to intervention (cat removal). It is important to note that these cat densities were much lower than those recorded in the cat-exposed source population (Predator Paddock) where cat density was 1.84/km^2 in January 2019, reduced (artificially) to 0.64/km^2 two months later (Moseby et al. 2020). A key difference between the Predator and Release Paddocks is that cats were not present when bettongs were initially translocated to the Predator Paddock but were added in shortly afterwards (West et al. 2018b) suggesting that a period of low or no predator density prior to exposure to cats may be beneficial. Intensive pre-release predator control to allow released animals a settling period may thus be advantageous. However, most deaths in the low cat density experiment occurred more than 200 days after release which does not support this suggestion.

Table 4 Survival (to collar removal) of translocated burrowing bettongs

	Cat-exposed		Cat-naïve	
	Survived	Died	Survived	Died
Release one (2017)				
Female	2	7	1	7
Male	1	9	0	12
Release two (2018)				
Female	6	8	8	6
Male	3	7	2	8
Total (%)	27.9%	72.1%	25%	75%

Collar removal occurred around 100 days after release for release one, and around 250 days after release for release two.

At moderate cat densities both cat-exposed and cat-naïve bettongs had low survival during the ca. 100 day tracking period in the Release Paddock and no bettongs were recorded on camera after nine months. This high mortality of both groups after release mirrors the findings of previous reintroductions of bettongs into areas with introduced predators (Bannister et al. 2016; Christensen and Burrows 1995; Moseby et al. 2011), but is at odds with a reintroduction of greater bilbies into the same area where cat exposed individuals survived for longer that cat-naïve individuals (Ross et al. 2019). In the present study, none of the measured physical traits conferred a survival advantage for bettongs at moderate cat densities suggesting that when predation rates are high, all individuals are at a similar risk irrespective of their physical traits.

In contrast to Release One, bettong sex had a weak influence ($P = 0.08$) on survival during Release Two, with males tending to die sooner. Males may have been at higher risk of encountering a cat during Release Two, when there was lower cat activity, because they undertake longer movements (Sander et al. 1997) and engage more actively in agonistic intra-specific interactions than females (Stodart 1966). In Release One, cat densities were higher and less mobile individuals (females) were possibly equally as likely to encounter cats.

During Release Two, when cat activity was lower, bettong survival was high until 200 days post-release. However, after 200 days, mortality increased sharply over a period of one month despite cat activity remaining stable over the post release period. This spike in predation could reflect a reduction in the availability of alternative prey leading to cats prey switching (Doherty et al. 2015) and targeting bettongs. Although there was no obvious reduction in rabbit activity, reptile activity was not monitored and the timing of the decline coincides with the onset of winter, while small mammal activity was slightly higher in the summer months immediately following the release, before declining in autumn. Alternatively, there may have been an incursion of cat(s) into the paddock, or cats (present within the Release Paddock) may have learned to hunt bettongs over time or reached an age and size where they could catch bettongs, which are at the upper end of the prey size range of cats (Doherty et al. 2017). Previous studies have found that male cats (Marlow et al. 2015) or large male cats (>4 kg) (Moseby et al. 2015) are more likely to kill difficult or large prey and can increase their hunting rate over time.

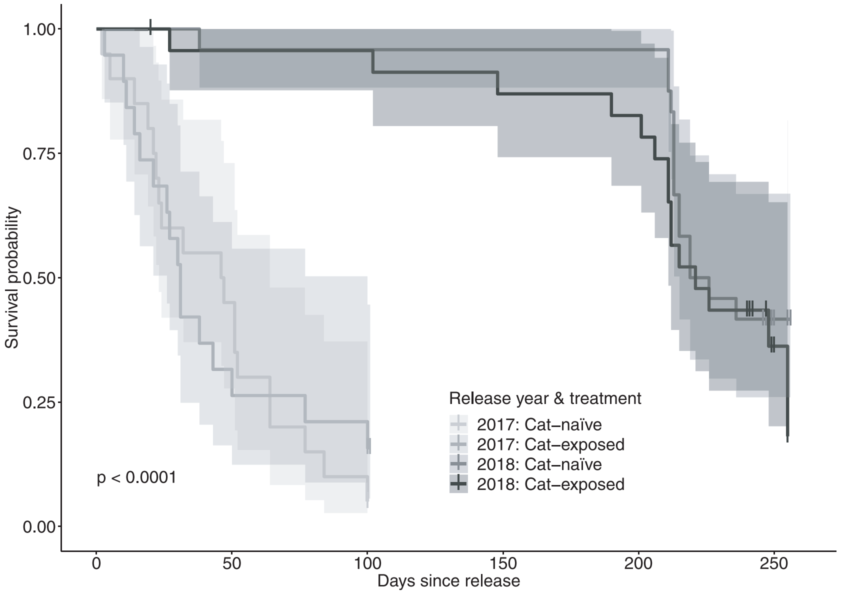

Figure 3 Burrowing bettong survival by release treatment and year.

Table 5 Results of Cox proportional hazard regression analysis for experimental burrowing bettong releases conducted in 2017 (n = 39, Concordance = 0.57 (SE = 0.06), Wald test = 1.79, 4 *df*, P = 0.78, R^2 = 0.05), and 2018 (n = 45, Concordance = 0.70 (SE = 0.06), Wald test = 12.45, 5 *df*, P = 0.03, R^2 = 0.24)

Release	Coefficient	SE	*P*-value
2017 (Release one)			
Treatment (cat-naïve)	−0.05	0.37	0.89
Sex (male)	0.46	0.37	0.22
Hind foot length (mm)	−0.03	0.06	0.57
Head length (mm)	−0.01	0.07	0.87
2018 (Release two)			
Treatment (cat-naïve)	−0.05	0.53	0.93
Sex (male)	0.71	0.41	0.08
Hind foot length (mm)	−0.26	0.09	0.004*
Head length (mm)	0.19	0.10	0.07
Proportion unique warren use	0.20	0.76	0.80

Significant (*) negative coefficients indicate that a variable decreased hazard, and hence increased longevity.

Increasingly dry conditions, owing to drought, may also have led to bettongs foraging further from their warrens (e.g. Dickman et al. 2010), and thus increasing their exposure to predators. However, bettongs in Release Two began breeding almost immediately after release, suggesting conditions were not unfavourable. The delayed spike in mortalities is interesting for reintroduction biology in the broader context because the critical period for most releases is the period immediately following reintroduction (Armstrong et al. 2017). Our finding that predation rates can increase sharply 200 days after reintroduction highlights and supports other studies showing predation rates on reintroduced prey can change dramatically over short time periods (Hardman et al. 2016).

Although West et al. (2018b) and Moseby et al. (2018) found physical and behavioural differences between populations of cat exposed and cat-naïve bettongs after only 18 months of cat-exposure, three years of cat exposure did not confer a survival advantage for reintroduced bettongs in this study. However, the results of Release Two, when cat activity was low, showed that hind foot length was a predictor of bettong survival and that individuals with longer feet survived for longer. Despite cat-exposed bettongs having longer hind feet on average, there was overlap with cat-naïve bettongs (Release Two hind foot length (range), cat-exposed = 100.3–109.3 mm, cat-naïve = 99.1–106.9 mm; Table 2) which may explain why hind foot length, rather than treatment *per se*, significantly increased survival. Larger hind foot length may confer a survival advantage by giving bettongs a locomotor advantage during escape. A previous study with a larger sample size found a significant difference in hind foot length between cat-exposed and cat-naïve bettongs (Moseby et al. 2018), however the difference in hind foot length in the much smaller sample size of the current study may explain why a significant effect of treatment on survival was not also found. West et al. (2018a) found that smaller bettongs foraged further from their warren and were more likely to die after release suggesting there may also be a link between size and movement, which could affect predation risk.

There may be several reasons why we recorded no post-release survival difference between the cat-exposed and cat naïve bettongs despite a survival difference being previously recorded in predator exposed bilbies at the same study site (Ross et al. 2019). First, although strong selection by predators can trigger rapid evolutionary changes (Réale and Festa-Bianchet 2003), the magnitude of the trait differences between our two populations may have been too small to have a fitness effect. Related to this, because the effect size on survival may be small, our sample size of 20–25 individuals in each treatment in each release may have been insufficient to detect significant differences. Either larger release groups and/or longer cat exposure may be required to enable survival differences to be detected.

Second, bettongs may simply be “outgunned” (Banks and Dickman 2007) and, despite significant trait changes, are unable to effectively respond to threats imposed by cats and other novel predators. Support for the “outgunned” hypothesis is provided by the fact that burrowing bettongs became extinct from mainland Australia, due primarily to predation by introduced foxes and feral cats (Short and Turner 1993). Further support for this explanation comes from the original source of our animals—an island where their populations had no exposure to terrestrial predators following the creation of these islands by rising sea-levels approximately 7000 years ago (Lewis et al. 2013). Indeed, it may be that three years of cat exposure is not long enough to counteract the effects of 7000 years of isolation and relaxed selection for anti-predator traits (Blumstein and Daniel 2005). Bilbies, in contrast, still exist in the wild in a number of places which suggests that they have developed anti-predator responses that allow them to co-exist with introduced predators (Steindler and Letnic 2021).

Third, behavioural differences between bettongs and bilbies may also contribute to the increased vulnerability of bettongs to introduced predators, because bettongs are highly social and live in permanent shared warrens (Sander et al. 1997), while bilbies tend to live alone in burrows (Russell 1984) and move burrows regularly (Moseby and O’Donnell 2003). These differences between bilbies and bettongs may increase the conspicuousness of bettongs, thus increasing the chance of cats detecting and then preying on them. A previous study found that bettongs which stayed closer to their warrens were less docile and had a greater chance of survival (West et al. 2018a), thus it is possible that individual personality traits play a role in post-release survival. Finally, bettong density was higher in the Cat-free Paddock than the Predator Paddock, a result that is to be expected due to the cat predation impacts within the Predator Paddock regulating the bettong population. This difference in bettong density may have contributed to the differences in morphology reported during the study, but separating out the effects of density-dependence (non-direct effects) and predation is difficult (Creel and Christianson 2008). However, the shifts in behaviour and morphology we report are consistent with responses to predation. Controlled experiments such as common garden experiments, where density, predation and maternal effects can be controlled for, are required and recommended in order to confidently identify predation effects.

In summary, our results show that ≥3 years of prior exposure to predators had no measurable effect on the survival of reintroduced bettongs and that individual attributes may not be important for survival when predator densities are too high, but that at low predator densities intraspecific differences are more apparent. Moreover, the contrasting effects of prior predator exposure on the fates of reintroduced bettongs (no effect, this study) and greater bilbies (significant positive effect, see Ross et al. 2019) highlights that prior predator exposure has the potential to improve anti-predator responses of reintroduced prey, but also that the efficacy or time of exposure required may vary between species, or that the co-existence thresholds of some species with introduced predators may be too low to be sustained in the wild. We used bettongs that were exposed to feral cats under natural conditions, thus our results are likely to be applicable to wild situations and relevant to a range of circumstances. We suggest that exposing populations to predators over longer time periods, monitoring divergence in traits and testing survival is required to determine whether pre-release predator exposure prepares animals with prolonged relaxation of predation pressure, like bettongs, for life with predators. Furthermore, the rapid failure of the reintroduction of bettongs at a moderate cat density and eventual failure of the reintroduction conducted at low cat density demonstrates that it is likely that some level of predator control will always be required prior to reintroduction including in situations where *in situ* exposure to predators has been conducted prior to release, in order for benefits of intraspecific variation in anti-predator traits to be realised.

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