



# The ‘Goldilocks Zone’ of predation: the level of fox control needed to select predator resistance in a reintroduced mammal in Australia

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## Abstract

A large component of the anthropogenic biodiversity crisis is the loss of animal species. In response, there has been significant investment in reintroductions of species to their historical ranges. Predation by native and exotic predators, however, remains a barrier to success. Over the past 200 years, Australia has seen the highest rate of mammal extinction on earth, with mammals within a critical weight range (CWR: 35 g–5.5 kg) most affected due to predation by exotic predators. Populations of some threatened species now exist only in Tasmania, offshore islands, or predator-proof sanctuaries. The next critical step is to return native populations outside of predator-free areas, ‘beyond-the-fence’, on the continental mainland. Given our current inability to completely remove exotic predators from mainland ecosystems, how can we achieve successful mammal reintroductions? A potential solution is to drive adaptation of reintroduced animals towards predator-resistance by exposing them to low levels of predation. We propose the concept of a ‘Goldilocks Zone’—the ‘just right’ levels of predation needed to drive selection for predator-resistant native species, while ensuring population viability. We experimentally reintroduced a mammal, the eastern bettong (*Bettongia gaimardi*), to mainland Australia, 100 years after its local extinction. Using an intense baiting regime, we reduced the population density of the red fox (*Vulpes vulpes*), the main factor behind the eastern bettong’s extirpation from the continent. Reducing bait take to 15% of previous levels allowed differential survival among bettongs; some surviving under 100 days and others over 450 (~4 times longer than some similar trials with related species). Surviving individuals were generally larger at release than those that died earlier, implying selection for larger bettongs. Our results suggest that reducing predation could establish a Goldilocks Zone that could drive selection for bettongs with predator-resistant traits. Our work contributes to a growing body of literature that explores a shift towards harnessing evolutionary principles to combat the challenges posed by animal management and conservation.

**Keywords** Invasive predator · Adaptation · Extinction · Predator naïveté · Reintroduction · Conservation · Predator management · Critical weight range · Beyond the fence

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## Introduction

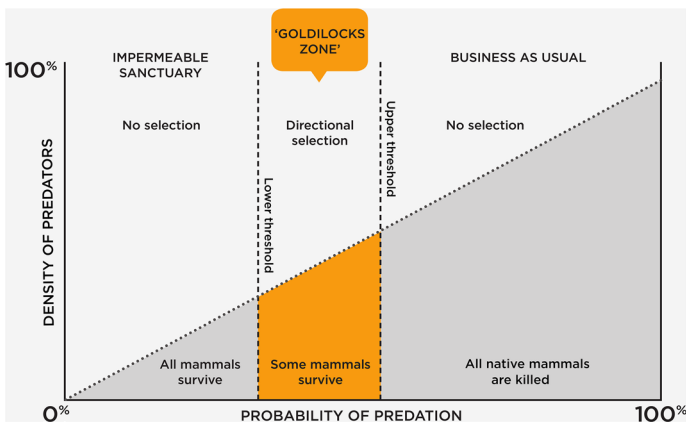
In the last 500 years, humans have caused a global wave of biodiversity loss, which includes mass extinction and population declines akin to those seen in the previous five mass extinction events in Earth's history (Ceballos et al. 2015). A huge component of this biodiversity loss is the loss of animal species, or 'Anthropocene defaunation' (Dirzo et al. 2014), caused by habitat modification, hunting and predation by exotic predators (Cardillo et al. 2005). Over the last 200 years, Australia has seen the highest rate of mammal extinction of all continents on earth (Woinarski et al. 2015). This extinction rate is driven, in part, by the predation of native mammals by exotic predators, such as the European red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*) (Kinnear et al. 2002; Moseby et al. 2011; Woinarski et al. 2015; Fairfax 2018; Radford et al. 2018). These predators have had devastating effects on native mammal species within a critical weight range (CWR) of 35 g–5.5 kg (Johnson and Isaac 2009; Radford et al. 2018). Native mammals that fall outside of this CWR are much less vulnerable to predation. In response to this severe decline of native mammals, there has been significant investment in the reintroduction of species to their historical range, following their local extinction (Armstrong et al. 2019; Berger-Tal et al. 2019). Most successful reintroductions of CWR mammals have occurred in places where exotic predators are absent or have been removed, such as on islands or into fenced sanctuaries (Legge et al. 2018).

The next crucial step is the return of native mammals outside of predator free areas, i.e., 'beyond-the-fence', on the continental mainland. A key aspect of this next step is the challenge posed by attempting reintroductions into ecosystems where CWR mammals will encounter the exotic predators that may have contributed to their original decline. Generally, conservationists have discounted the idea that native mammals and exotic predators can co-exist (Bode 2018). As a result, the presumption is that, for CWR mammals to be returned to their historical range, exotic predators need to be eradicated completely from the landscape. Achieving complete eradication, however, is extremely difficult. Most control programs are unable to remove exotic predators completely or permanently (Gentle et al. 2007; Saunders et al. 2010). There is evidence, from some contexts, that returning CWR mammals beyond-the-fence can work, and the potential for co-existence is not without precedent. Moseby et al. (2019), for example, demonstrated that populations of the burrowing bettong (*B. lesueur*) and the bilby (*Macrotis lagotis*) were able to persist in the presence of low numbers of one of their primary predators, the cat. Also, reducing foxes to low levels has been shown to result in increases in abundances of the brush-tailed bettong (*B. pennicillata*) (Kinnear et al. 2002; Orell 2004), and several other Australian CWR mammals (Morris et al. 1995; Sinclair et al. 1996; Hayward 2012; Robley et al. 2014). The co-existence of exotic predators and native mammals, therefore, offers the potential for a return of native CWR mammals to the broader landscape in Australia.

The challenge of reintroducing native CWR mammals beyond-the-fence, however, is amplified by 'refuge naïveté'. Most reintroduction programs source animals from predator-free sanctuaries where individuals may have lost any predator aversion that existed previously (Jolly et al. 2018). This refuge naïveté, an unintended consequence of measures to conserve at-risk species (Orrock 2010; Jolly et al. 2018), creates a 'wicked problem'—species can either be conserved in fenced sanctuaries or on offshore islands, causing them to lose the behavioral adaptations (or characteristics) required to survive beyond-the-fence, or they can be released beyond-the-fence and face total extinction as a result of exotic predators that cannot be removed from the landscape.

A proposed solution to the wicked problem is to drive reintroduced animal adaptation towards predator resistance by exposing them to low levels of predation (Osmond et al. 2017; Moseby et al. 2018). If these traits are heritable, they could eventually result in a more predator-resistant population. A challenge for this type of work is identifying the densities of predators that populations of prey species can tolerate (Moseby et al. 2019). The level of predation should be enough to drive directional selection towards individuals that have traits that increase their likelihood of survival i.e., ‘predator resistance’, without threatening the viability of the prey population (Osmond et al. 2017; Moseby et al. 2019). We introduce the concept of the ‘Goldilocks Zone’ of predation (Fig. 1; derived from ‘Goldilocks and the three bears’ children’s fable, henceforth, the Goldilocks Zone). We apply the concept of the Goldilocks Zone to predator densities with the aim of achieving predation levels that are ‘just right’ to drive adaptation towards predator resistance in the reintroduced species. If the predation is too high, then all individuals will be preyed upon without the opportunity to pass heritable traits on to their offspring. If predation is too low, however, the traits crucial for predator-resistance, will not be selected for and animals will develop maladaptive refuge naïveté. Identifying and achieving the Goldilocks Zone is an important step for reintroduction programs that aim to return mammals beyond-the-fence. It should be measurable and achievable for each CWR species, thereby giving managers a quantitatively based target.

In this paper, we explore the Goldilocks Zone for the eastern bettong (*Bettongia gaimardi*) as part of an experimental reintroduction conducted within an adaptive management framework (Batson et al. 2015; Wilson et al. 2020). The eastern bettong was extirpated on the Australian mainland due to predation by foxes and feral cats and was last thought to inhabit the continent over 100 years ago (Short 1998). It now survives only in the island state of Tasmania (Taylor 1992), and (at the time of writing) inside two predator-free sanctuaries; one in the Australian Capital Territory (ACT) (Batson et al. 2016) and one in Victoria.



**Fig. 1** A conceptual diagram of the Goldilocks Zone of predation pressure. To drive selection, the level of predation should be enough to select individuals that have traits that increase their likelihood of survival. If the predation is too high (to the right of the upper threshold of the Goldilocks Zone), then all individuals will be preyed upon without the opportunity to pass heritable traits onto their offspring (i.e. business-as-usual). If predation is too low (to the left of the lower threshold of the Goldilocks Zone), then those traits crucial for predator resistance will not be selected for in individuals (i.e. predator-proof sanctuaries)

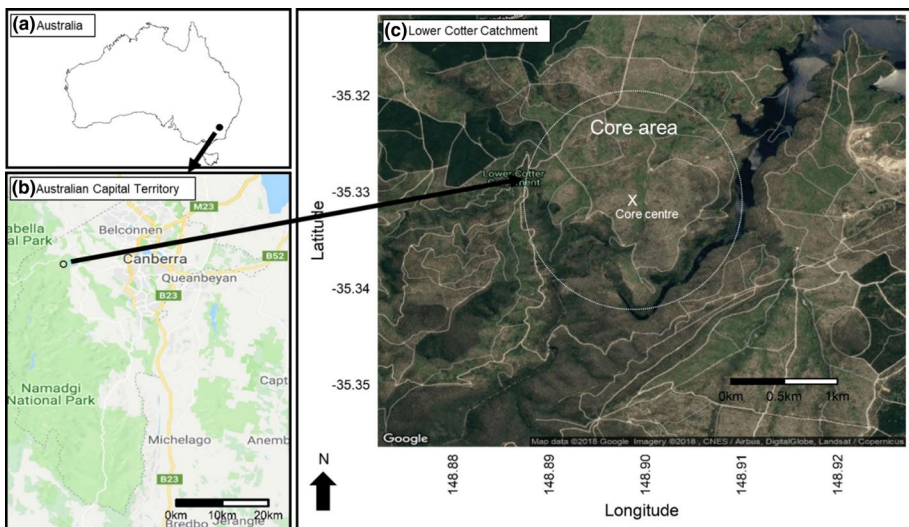
## Methods

### Experimental design

The complexity of returning CWR mammals, such as the eastern bettong, beyond-the-fence means that it may not be possible to successfully restore populations in a single step. Our reintroduction experiment, therefore, was undertaken within an adaptive management framework and used the Translocation Tactics Classification System (TTCS) (Batson et al. 2015; Wilson et al. 2020). The TTCS aims to improve reintroduction success by trialing ‘tactics’ that are either focused on the reintroduced animal (e.g., selecting suitable founders) or the threats in the environment (e.g., removing predators). The aim of the experimental reintroduction was to understand conditions that facilitate the adaptation of a population of bettongs, beyond-the-fence, towards a population that can co-exist with foxes and feral cats. Studies have shown that, despite not sharing any recent evolutionary history with exotic predators, mammals in the *Bettongia* genus can develop wariness to them (Saxon-Mills et al. 2018). In this experiment, foxes were controlled to low levels—our key environment-focused tactic within the TTCS. Our program included an adaptive fox control and monitoring program which sought to reduce the threat of predation, whilst simultaneously reintroducing bettongs. With the fox control program, we aimed to determine the relative density of foxes at which bettongs could experience selection for individuals that possess predator-resistant traits.

### Study area

The study area is in the Lower Cotter Catchment (LCC) in the ACT, Australia (longitude: 148.9000, latitude:  $-35.33700$ ) (Fig. 2). The area forms part of the watershed for the



**Fig. 2** The Australian Capital Territory (ACT) within Australia (a); the location of the Lower Cotter Catchment within the ACT (b); and the study area including the ‘Core area’ where we released bettongs (c) (maps downloaded from Google). The circled core area shown is roughly 2 km in diameter

Cotter Dam Reservoir, which supplies water to Canberra, ACT. The LCC was declared a reserve in 2014. There has been significant investment in the restoration of native species following bush fires in 2003 that destroyed the large commercial *Radiata* pine plantation. Restoration has included planting native vegetation, weeding for blackberry and pine wildings and controlling pest animals such as rabbits (*Oryctolagus cuniculus*) and pigs (*Sus scrofa*) (ACT Government 2018). The area is traversed by service roads, most of which are behind locked gates, used to prevent erosion caused by trail bikes and off-road vehicles.

## Fox baiting and monitoring

Currently, there are no new ‘game changing’ fox control technologies in the pipeline, therefore, the focus remains on the refinement of fox control regimes. There are several successful beyond-the-fence projects in Australia that have developed effective control regimes using current technology (see above); however, each situation is different, and there are no a priori guarantees of success. All beyond-the-fence projects, therefore, should be the subject of adaptive experimentation (Parkes et al. 2006).

We conducted a comprehensive adaptive fox control regime from April 2015 until January 2018 using a variety of sodium fluoroacetate (hereafter 1080) poison baits. Poison baiting is considered to be one of the most cost-effective techniques for fox control (Saunders et al. 1995). Our approach was to create a buffer zone around a core area (Thomson et al. 2000; Marlow et al. 2016) where we would reintroduce bettongs (Fig. 2). In designing our fox control program, we used the topography of the landscape, with the core zone situated adjacent to the reservoir to eliminate fox invasions from the south and east. After an initial knockdown of foxes across the whole area, including the core, we hypothesized that most incoming foxes from the surrounding landscape would be killed before reaching the core area. Any that were able to reach the core area would provide the low level of predation needed for selection for predator-resistant bettongs. Our baiting frequency was more intensive (> four times) than the previously recommended frequency (6–12 times per year) to protect vulnerable fauna from fox predation (see Table S1 for details) (de Tores and Marlow 2012; Marlow et al. 2015b, 2016).

## Baiting phases

Our baiting program consisted of three phases (for details see Fig. S1). Phase 1 (May–August 2015) involved an initial knock down of the fox population using 1080 buried ground baits of various commercial and non-commercial types (bait sites = 74). This phase was followed by Phase 2 (September 2015–June 2017) which involved continued baiting using 1080 ground baits (bait sites = 132), but we adapted the regime and spatial arrangement to concentrate baits where foxes were more likely to take baits. Phase 2 saw the introduction of M-44 1080 ejector baits, designed to deliver 1080 directly into the fox’s mouth (ejector sites = 24). Finally, in Phase 3 (July 2017–January 2018) we increased ejector baits (ejector sites = 90) whilst continuing ground bait poisoning, but at longer time intervals and varying the location of baits (bait sites = 168).

We buried 1080 ground baits 8–10 cm into the ground at roughly 500 m intervals along service roads in the study area. We checked baits every 3–7 days and replaced them if they were disturbed or taken. We replaced all baits that were not disturbed or taken within 21 days. Throughout the baiting program, as part of our adaptive approach, we adjusted the locations and intensities of baits in response to on-the-ground indications of increased

fox presence. We recorded the coordinates of every ground bait location, the length of time that the bait had been out for and whether the bait was disturbed or taken.

We introduced M-44 ejector baits loaded with 1080 capsules in September 2015 (Phase 2). M-44 ejectors use a spring-activated system to propel the contents of a capsule into a predator's mouth (Lapidge 2004). Ejectors offer an efficient means with which to kill foxes and also circumvent the problem of foxes caching and not consuming the poison bait (Kay et al. 1999; Lapidge 2004). Our intention, when introducing ejector baits, was to reduce the labor costs needed to service the baiting program and reduce caching (burying of baits for future consumption by the fox) that can occur with ground baits.

### Camera trapping monitoring network

Alongside the baiting program, we conducted a camera trapping regime to detect foxes and other predators present in the area (May 2015–January 2018). Our intention was to provide an independent measure of fox numbers in the landscape than that provided by using bait take. We used LTL-5610 camera traps (LTL Acorn) (in total 59 sites with a maximum of 35 cameras used concurrently) which we placed a few meters off the side of service roads to avoid detection by vandals in the area. We used camera traps continuously throughout the study although there were rare occasions when the cameras could not be operated. We used various scent lures (tuna oil, fox urine, peanut butter, oats) to attract foxes to the camera traps. We recorded animal presence or absence in each 24-h period that the camera was operational.

### Bettong releases

During the study period, we released 46 bettongs in stages (two separate cohorts) from August 2016 until July 2017. The first 27 animals were released between August and November 2016 and the second 19 animals between May and July 2017. We sourced bettongs from two sanctuaries within the ACT: The Mulligans Flat Woodland Sanctuary and Tidbinbilla Nature Reserve (Table S2). Before transfer to the LCC, the bettongs were weighed and had their pes (foot) length measured. We monitored bettongs using VHF radio tracking collars to confirm their survival or to locate them in cases of mortality. All methods were carried out in accordance with relevant guidelines and regulations. This project, including the experimental protocols, was approved by the ANU Animal Ethics and Experimentation Committee (Protocol A2015/73).

### Statistics

We determined the Goldilocks Zone in three sequential steps. Firstly, by monitoring the fox population density, then by identifying groups of bettongs classified according to their survival time, then lastly, by calculating the fox density required to potentially drive selection for bettongs that survive longer.

### Fox monitoring

To test the effectiveness of our regime we fitted generalized linear mixed models using the 'lme4' package (Bates et al. 2015) in R (R Core Team 2020), using three response variables: (1) ground bait take; (2) ejector bait take; and, (3) camera detections. For the ground

and ejector bait take data, our response variables were binomial (0 = not taken, 1 = taken). Baits were only counted once—if, for example, a bait was checked every 3–7 days, and was replaced after 21 days, and not taken, it was counted as a zero. On the other hand, if the bait was taken on day 7, for example, it was counted as a one. To account for the varying amounts of time that each bait was out in the landscape for, we included a ‘*time bait out for*’ covariate (Table S3) in all models. Cameras’ response variables were standardized as camera detections per day across all cameras. For all models, we accounted for *effort* by calculating an index of bait density at each bait location for each month using the ‘*density.ppp()*’ function in the ‘*spatstat*’ package (Baddeley et al. 2015) in R (Table S3). For this variable, baits in areas with a relatively large number of nearby baits were weighted higher than those in areas with a smaller number of baits with fewer replications. The ‘*effort*’ variable was rescaled to have the same mean (0) and standard deviation (1). Each response variable was binomial, therefore, we assumed binomial distributions and tested for overdispersion for all models.

To test the effect of the fox control program over time, we modelled each of our response variables against *month* as a factor variable (Table S3). To determine whether our core zone approach was effective we wanted to test the effect of distance to the center of the core zone for all three response variables. To detect whether this distance changed over time (i.e., whether in the first year there was no relationship, whereas after baiting there was a positive relationship between distance and our response variables), we tested the interaction between *distance to core* (continuous) and *year* (factor) (Table S3). To determine from where in the landscape foxes might be entering the core, we tested *direction* (factor) from the center of the core [North (315°N–45°N), South (135°N–225°N), East (45°N–135°N), West (225°N–315°N)], as well its interaction with *year* (Table S3). In all models, to account for repeated measures, we used *location* as a random effect (location of bait, Table S3). For the purposes of plotting we predicted values where the ‘*time bait out for*’ variable was set to 14; i.e., that our values for probability of bait take were predicted if each individual bait was available for 14 days.

## Identifying bettong survival groups

We nominated the 18th of January 2018 as the cut-off date for the study period—i.e., any surviving bettongs’ ‘*survival time in days*’ would be calculated from its release date until that date. We split bettongs into two cohorts dependent on how many days since release each individual bettong survived. This splitting was to avoid skewing the data towards bettongs that survived for fewer days, simply as a result of their more recent release. This splitting resulted in two cohorts (cohort 1:  $n=27$ , cohort 2:  $n=19$ ) (Table S2). Individuals in Cohort 1 ( $n=27$ ) had 440 or more possible days to survive and individuals in Cohort 2 ( $n=19$ ) had between 178 and 240 days to survive (up to the end of the study period).

To classify bettongs into groups of differential survival times we analysed the distribution of survival times for the two cohorts described above. To do this analysis, we fitted density estimates of Gaussian finite mixture models (Fraley and Raftery 2002) using the ‘*mclust*’ (Scrucca et al. 2016) package in R (R Core Team 2020). We fitted mixture models to both cohorts and compared their AIC scores to corresponding fits of unimodal Gaussian distribution fits. The mixture models were considered to be better fits than the unimodal models if their AIC scores were less than those of the unimodal Gaussian distribution fits by two AIC scores or more (Table S4). We identified three bettong groups, as determined by the distribution of survival times of the bettongs: low, high and very high survivorship

(Costello et al. 2016). This pattern may have indicated a possible first step in selection for bettongs with resistance to predation.

## Determining the Goldilocks Zone

To identify the Goldilocks Zone, we needed to calculate several variables from our data. Firstly, for each month, and in each survivorship group, we determined how many bettongs were alive in the study area in each month, and how many of those were preyed upon. For clarity in further analyses, we grouped the high and very high survivorship groups together to make two groups (low and high + very high survivorship groups). We then calculated a ratio of deaths per month for each of two survivorship groups by dividing bettong deaths by the number of bettongs in the population per month for each group. Secondly, we calculated a proxy for fox density by estimating values (probability) from the generalized linear mixed models of ground bait take, ejector activation and camera detection as our response variables, setting the ‘*time bait out for*’ variable at 14 (see above). We also included *distance to core* as a covariate in the model, thereby allowing us to predict values of bait take within the perimeter of the core area, i.e., within 1000 m of the center of the core. We then fitted a linear model of logit (ratio of deaths per month) against the interaction of our measures of fox density (bait take, ejector activation or camera traps) and a factor variable of two groups (low, high + very high survivorship).

To demonstrate the relationship between the strength of selection and fox density, we first calculated selection strength in each month as the log of the ratio of the odds of survival in the high group divided by the ratio of odds of survival in the low group [ $\log(\text{odds ratio})$ ]. We used the Haldane-Anscombe correction (adding 0.5 to each value) to avoid errors with the presence of zeroes in the odds ratio contingency table (Lawson 2004). We then fitted a linear model of selection strength against our measures of fox density.

All analyses and plotting was completed in R (R Core Team 2020) using the ‘lme4’ (Bates et al. 2015), ‘ggplot2’ (Wickham and Seidel 2016), ‘spatstat’ (Baddeley et al. 2015), ‘geosphere’ (Hijmans 2019), ‘ggmap’ (Kahle and Wickham 2013), ‘ggpubr’ (Kassambara 2020), ‘AICcmodavg’ (Mazerolle 2019) and ‘boot’ (Davison and Hinkley 1997; Canty and Ripley 2020) packages.

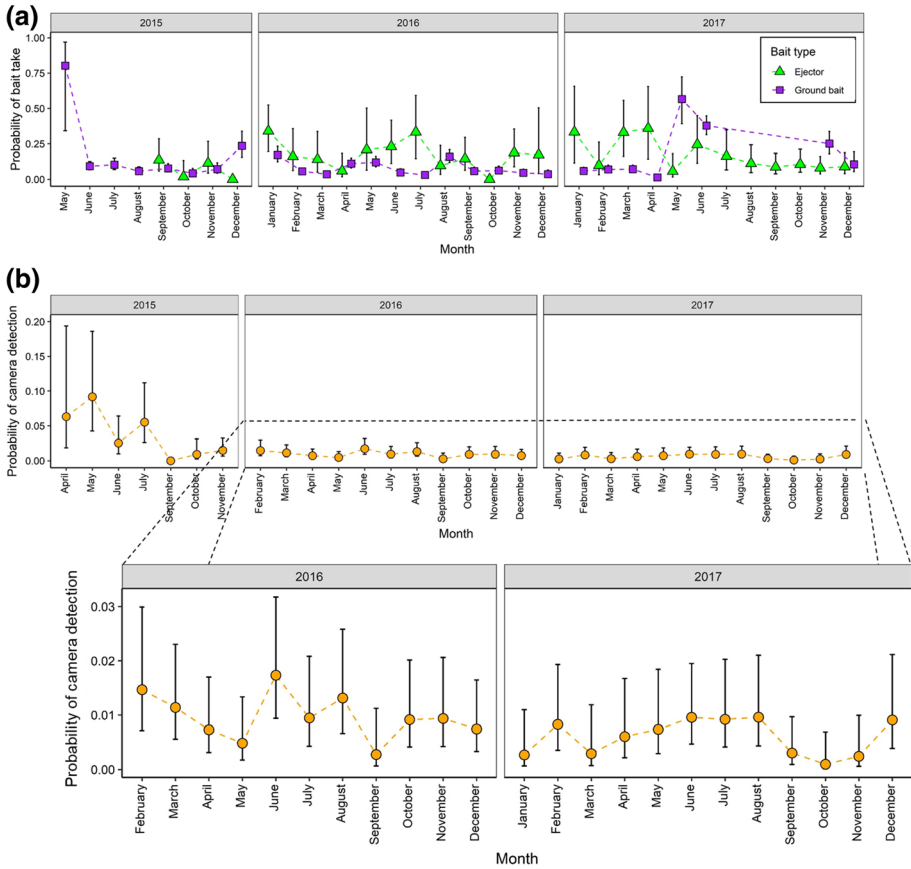
## Results

### Fox baiting and monitoring

We used 7047 buried ground baits, 1483 of which were taken, and 2408 ejectors, 389 of which were activated. Cameras were operational for the equivalent of 19,218 days (number of cameras  $\times$  the number of days they were active), with foxes detected on 450 of those days.

Both ground bait-take probability, and camera detection probability, indicated that fox activity was highest in April and May 2015 (Fig. 3). Fox activity was lower from then for two years until May 2017 when ground bait-take spiked and remained relatively high until December 2017 (Fig. 3a). Neither ejector activation probability nor camera detection probability mirrored this pattern (Fig. 3b) with both remaining low throughout 2016 and 2017. Ejector activation probability was very low in late 2015, when most ejectors were within the core area (Fig. 3b).

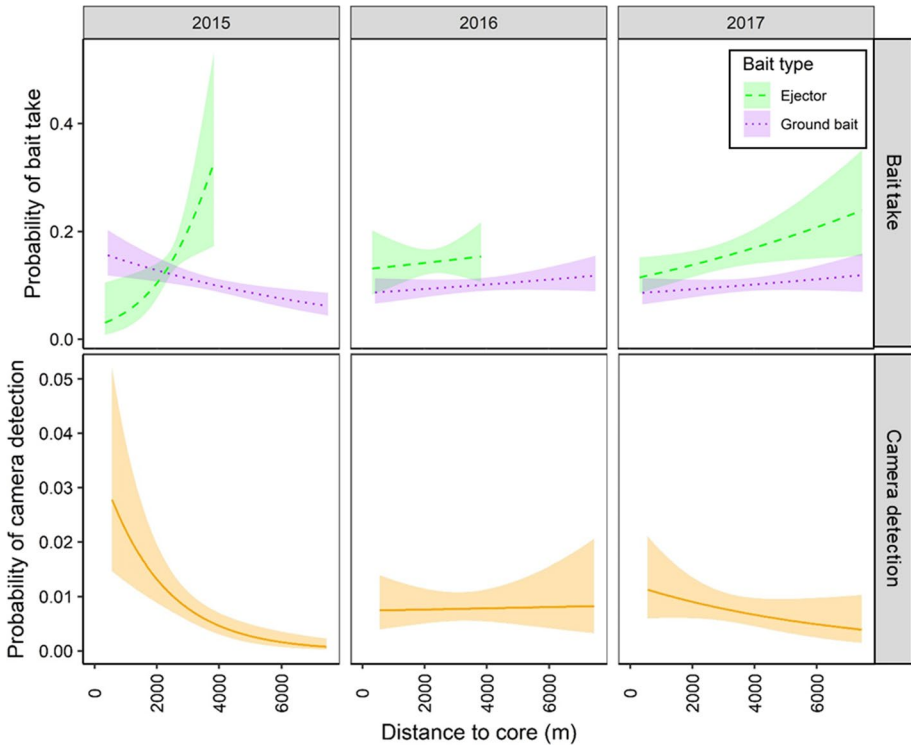




**Fig. 3** Estimated probabilities of ground bait and ejector activation per 14 days (a) and camera detection per day (b). Note the divergence between ground baits and ejectors from May 2017. Values indicated are estimated probabilities on the response scale using generalized linear mixed models (ground bait take  $p < 2.2e^{-16}***$ , ejector activation  $p = 1.475e^{-8}***$ , camera detections  $p = 4.38e^{-13}***$ ). *Effort* [in all models (a–c)] and *time bait out for* [bait models in (a)] were accounted for in the models. Models were predicted using the mean value for the time that there were available to foxes (12 days for ground baits, 16 days for ejector baits). Ground bait take and ejector bait activation were calculated in separate models but are shown on the same plot (a). The zoomed plot (b) shows camera detection probabilities in 2016 and 2017 on a different scale to that shown in the main plot. Error bars represent 95% confidence intervals

Ground bait-take probability was highest near to the core in 2015, declining with increasing distance from the core (Fig. 4). Ejector bait activation probability showed an opposite pattern in 2015 (Fig. 4), increasing from the center of the core to the edge of the experimental area. In 2016 and 2017, in contrast to 2015, ground bait-take probability rose with increasing distance from the core. Camera detection probabilities were consistent with ground bait-take probabilities in 2015 and 2016; however, in 2017, camera detections were more probable nearer to, rather than further from, the core (Fig. 4).

Ground bait-take probability was highest at locations east of the core in 2015 and 2016 (Fig. 5). In 2017, however, ground bait-take probability was similarly high in the north and west, but comparatively lower in the south (possibly indicating that the Cotter Dam Reservoir acted as a barrier to foxes). Ejector activation probability did not show a similar

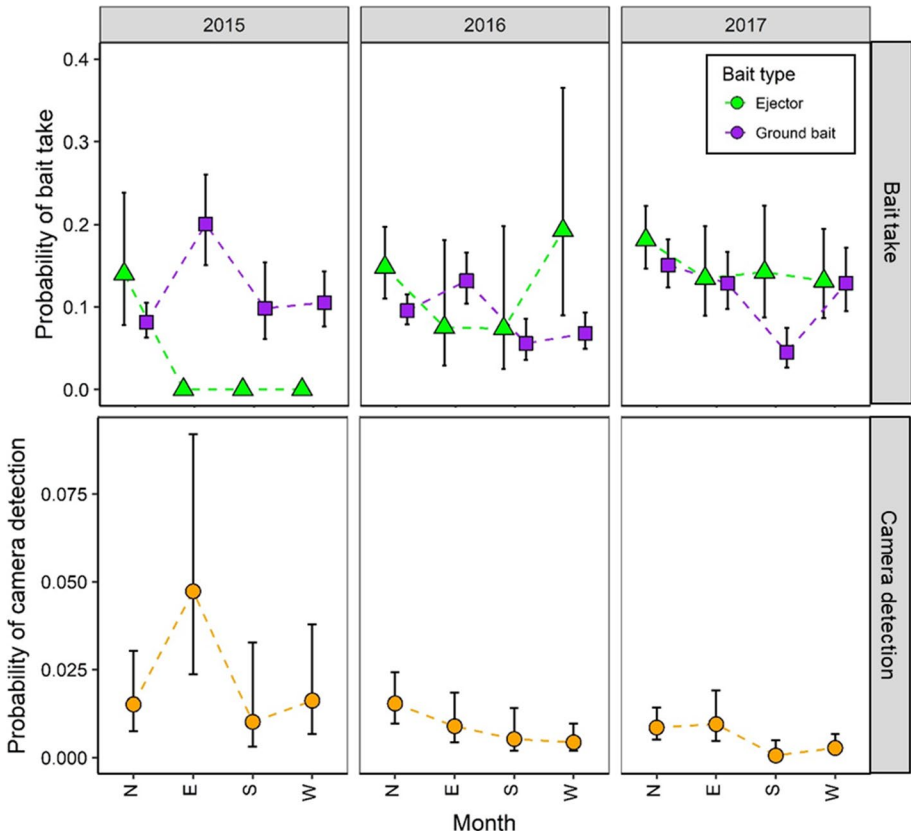


**Fig. 4** Estimated probabilities of ground bait take per 14 days (top row), ejector activation per 14 days (top row) and camera detection per day (bottom row) at increasing distances from the center of the core. For an effective regime, we aimed for probabilities to be low at the core (i.e. probabilities might increase with an increase in distance to the core). Values indicated are estimated probabilities on the response scale using generalized linear mixed models (ground bait take  $p < 2.2e^{-16***}$ , ejector activation  $p = 9.646e^{-8***}$ , camera detections  $p = 3.742e^{-13***}$ ). Models account for *effort* [in all models (a–c)] and *time bait out for* [bait models in (a)]. Ground bait take and ejector bait activation were calculated in separate models but are shown on the same plot. Errors represent 95% confidence intervals. Ejector fits are truncated in 2015 and 2016 because the maximum distance that ejectors were from the core center in those years was 3850 m

pattern to ground bait take in any year. Camera detection probabilities were similar to ground bait-take probabilities throughout (Fig. 5).

### Bettong survival groups

Bettongs demonstrated multimodal distributions of length of survival indicating that they were subject to a strong selective force (Fig. 6). Predation, mainly by foxes, resulted in two distinct groups of bettongs—those that avoided predation and those that did not. We analyzed the two separate cohorts based on the length of time that bettongs could potentially survive (i.e., the end of study date minus the release date); cohort 1 (440 days or more,  $n = 27$ ) and cohort 2 (between 178 and 240 days,  $n = 19$ ). Cohort 1 split into three groups with three levels of survival: 47% of bettongs surviving under 170 days, 34% surviving between 170 and 350 days and 19% surviving beyond 350 days (i.e., 53% over 170 days; Fig. 6a). Cohort 2 split into two groups with two levels of survival: 42% surviving less than

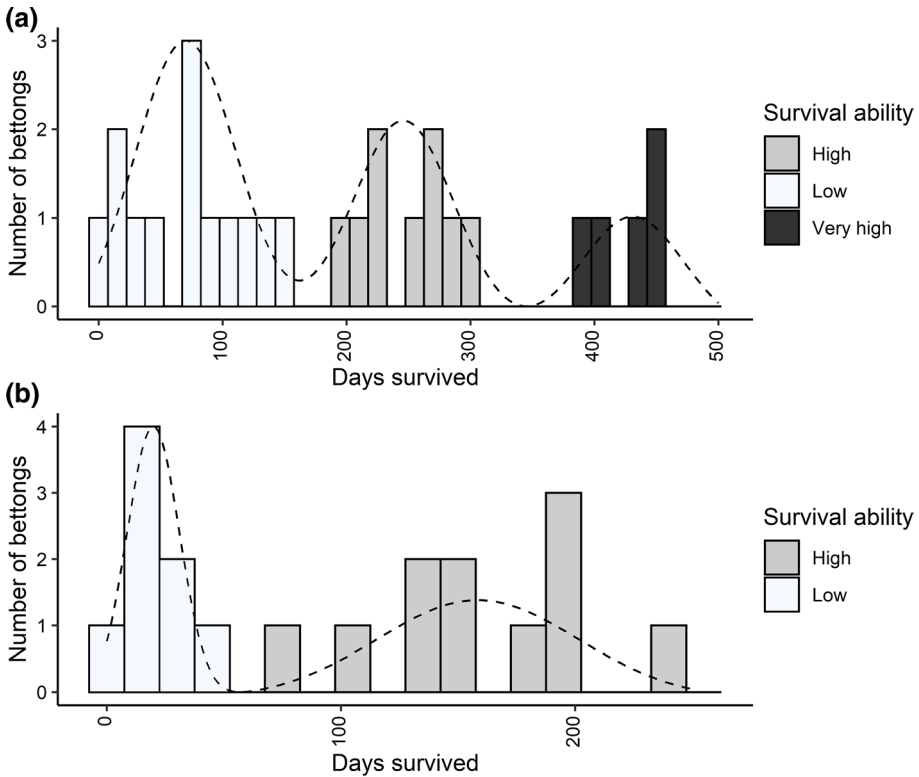


**Fig. 5** Estimated probabilities of ground bait take per 14 days (top row), ejector activation per 14 days (top row) and camera detection per day (bottom row) at different directions from the center of the core. Values indicated are predicted probabilities on the response scale using generalized linear mixed models (ground bait take  $p < 2.2e^{-16}***$ , ejector activation  $p = 1.422e^{-5}***$ , camera detections  $p = 6.740e^{-13}***$ ). Models account for *effort* [all models (a–c)] and *time bait out for* [bait models in (a)]. Ground bait take and ejector bait activation were calculated in separate models but are shown on the same plot. Error bars represent 95% confidence intervals

50 days and 58% surviving beyond that (Fig. 6b). Release weight was the only predictor of survival and this relationship was only the case for cohort 1 (see Supplementary materials for other variables tested). Generally, in cohort 1, the heavier the bettong at release, the longer it was likely to survive ( $p = 0.045$ ) (Figs. S3, S4). Bettongs in the *very high* survival group in cohort 1 were all at least 1.535 kg and the two heaviest bettongs demonstrated *high* survival (Fig. S4).

### The Goldilocks Zone

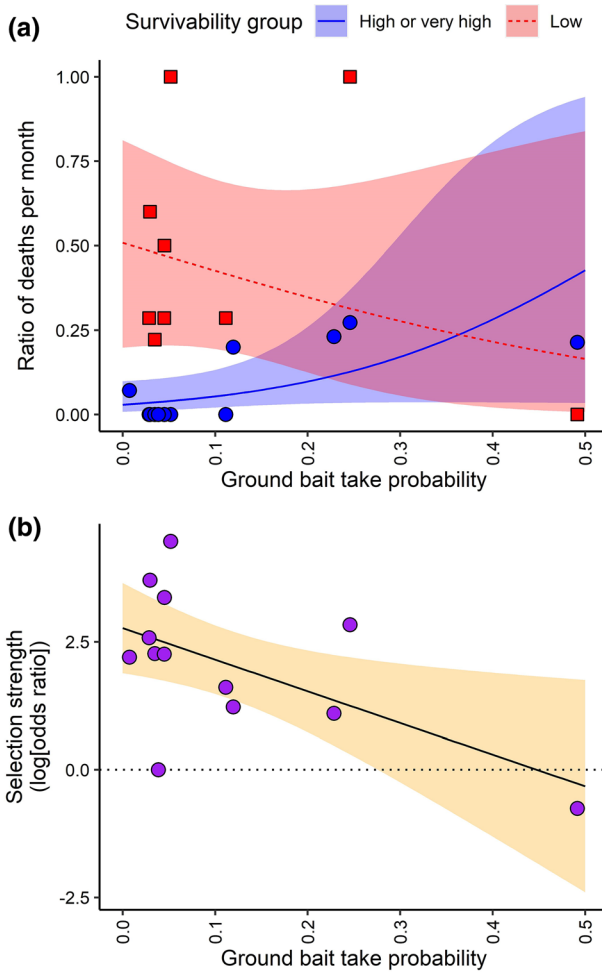
Ground bait-take probability showed a significant positive relationship with the ratio of bettong deaths per month in the high or very high survivorship group (Fig. 7a). There was no relationship, however, between ground bait-take probability and the ratio of bettong deaths in the low survivorship groups. That is, bettongs in the low survivorship



**Fig. 6** Survival distributions for bettongs in cohorts 1 **(a)** and 2 **(b)**. **a** Represents bettongs that had 440 days or more in the release site ( $n=27$ , cohort 1); and **b** represents bettongs that had 178–240 days in the release site ( $n=19$ , cohort 2). Survival ability groups comprised of *low* (47%), *high* (34%) and *very high* (19%) for cohort 1 **(a)** and comprise of *low* (42%) and *high* (58%) for cohort 2 **(b)**. The distribution density curve has been rescaled to overlay the histogram of survival

group were preyed upon regardless of the ground bait-take probability, whereas those in the high survivorship group were able to survive in the core area of up to about a 0.12 probability of bait take per 14 days. The upper threshold of the Goldilocks Zone in our study, therefore, was below a 0.12 chance/per 14 days of ground bait take in the core area. Given that bait take was estimated to be 0.8 per 14 days at the start of the program (Fig. 3), we estimate the upper threshold to be a reduction of fox activity to around 15% of the background activity of foxes. Selection strength showed a significant negative relationship with bait take ( $p=0.036$ ,  $F_{1,11}=5.684$ , adjusted  $R^2=0.281$ ), i.e., the strongest selection for fox-resistant bettongs was when fox density was lowest.

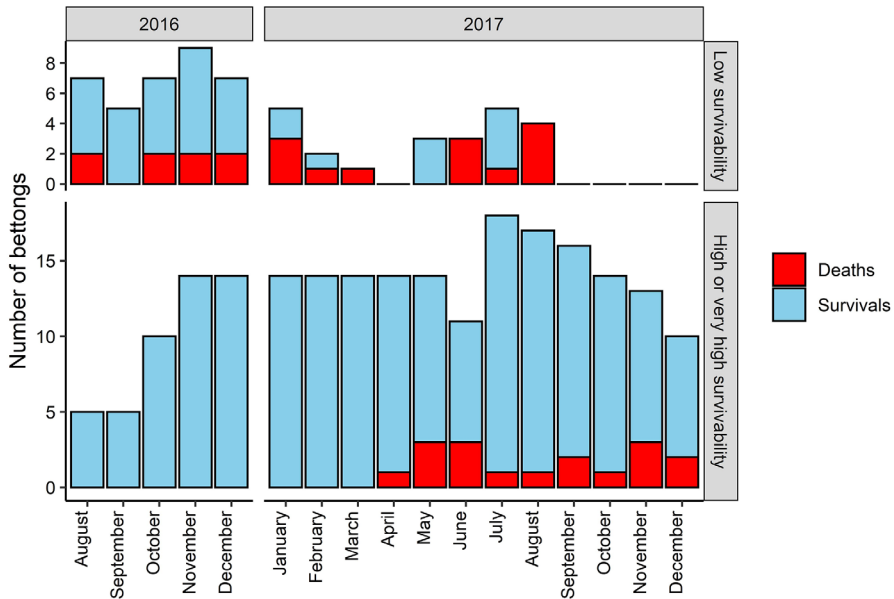
Those bettongs in the high and very high survivorship group survived through most of 2016 and into 2017 until the ground bait-take spike in May 2017 (Figs. 3, 8). Bettongs in the low survivorship group, on the other hand, were consistently preyed upon from when they were released and throughout 2016 and 2017, regardless of the level of ground bait take, whether that is at low or high bait-take rate (Figs. 3, 8). There was no relationship between either bettong group and ejector activation probability and camera detection probability.



**Fig. 7** The relationships between estimated ground bait-take probability against the ratio of bettong deaths per month for the two groups of bettong survivability **(a)** and selection strength **(b)**. The fit in **a** is estimated from a linear model of logit (ratio of deaths per month) against the interaction of ground bait-take probability and survivability group ( $p=0.0138$ ,  $F_{3,19}=4.609$ , adjusted  $R^2=0.330$ ). Ground bait-take probabilities were calculated using a mixed model with the scaled *distance to core* as a covariate with values predicted for distance to core values of 1000 m (i.e. the outer boundary of the core). Circular and square points represent the high or very high survivability and low survivability groups respectively. The solid blue line shows that deaths increase as bait take increases and that only above a 0.12 chance of bait take per 14 days do bettongs in the high or very high survivability group become preyed upon. In contrast, bettongs in the low survivability group are preyed upon at very low bait-take probabilities. The ratio of deaths per month was back transformed to its original scale for plotting. The fit in **b** is estimated from a linear model of the log of the ratio of the odds of survival in the high group divided by the ratio of odds of survival in the low group [ $\log(\text{odds ratio})$ ] against ground bait-take probability ( $p=0.036$ ,  $F_{1,11}=5.684$ , adjusted  $R^2=0.281$ )

## Discussion

Predation is a key reason many reintroduction programs worldwide fail (Moseby et al. 2011, 2015). Predator naïveté among reintroduced animals compounds the problem by



**Fig. 8** The numbers of deaths and survivals each month in each of the bettong survivability groups. Throughout 2016 and early 2017 when ground bait take was relatively low (Fig. 3), there were only deaths in the low survivability group (top row). Only when there was a spike in ground bait take around May 2017 (Fig. 3), did bettongs in the high or very high survivability groups become preyed upon (bottom row).

making reintroduced animals more susceptible to predation. Conservationists are faced with a ‘wicked problem’ whereby species gain refuge naïveté if conserved in fenced sanctuaries or on offshore islands but face total extinction in the wild because of exotic predators that cannot be removed from the landscape. The Goldilocks Zone of predation concept could potentially address this wicked problem. We postulate that establishing some level of predation prior to reintroduction could drive selection for predator-resistance and should be a key component in re-establishing native CWR mammals beyond the fence. In the following discussion, we examine the results of our study and how they might demonstrate the Goldilocks Zone concept. We then look at how this concept can contribute to conservation of CWR mammals in Australia.

Here, we have demonstrated how it is possible to reduce exotic predators to a level that allows reintroduced mammals the opportunity (time) to experience selection over the short term. Encouragingly, several individuals survived until the end of the experiment, over a year after their release (>450 days). This survival time was around four times longer than trials with the related burrowing bettong (Bannister et al. 2016; Moyses et al. 2020). Our result offers real hope that continued refinement of tactics, in a series of steps within an adaptive management framework (Batson et al. 2015; Wilson et al. 2020), could ultimately result in establishing *Bettongia* species and other CWR mammals in more places beyond-the-fence on mainland Australia.

A crucial aspect of the Goldilocks Zone concept is establishing its upper threshold of predation. Below this threshold, animals are selected for traits that allow them to resist predation, but when the threshold is crossed, too many individuals are killed and the population will be driven to extinction before selection can take place. For the majority of the time of the study (mid 2016–mid 2017), bettongs were living freely in the presence of

foxes. When predation levels increased around May 2017 (demonstrated by bait-take data), those predator-resistant bettongs succumbed to predation. We interpret that, at this time, the upper threshold of the Goldilocks Zone was crossed.

Quantifying the upper threshold (Fig. 1) of the Goldilocks Zone is complex. In our experiment, we estimated the upper threshold to be approximately around 15% of background predation levels (80% bait take per 14 days). This estimate is subject to caveats. Firstly, our estimates of the initial background fox levels, predator activity and bettong survival of are all subject to error, leading to uncertainty on this specific figure. Secondly, background levels of foxes are subject to fluctuations throughout the year and between years. Fox numbers usually increase between late spring and autumn (November to March in Australia) with the emergence of juveniles. Their numbers then decrease in winter (June–August in Australia) (Saunders et al. 1995). All of this uncertainty makes determining a generalizable figure for the upper threshold of the Goldilocks Zone difficult.

The Goldilocks Zone concept also requires a lower threshold of predation (Fig. 1). To avoid maladaptive refuge naïveté, animals must be exposed to enough predation pressure to drive selection and adaptation. Demonstrating the lower threshold would involve monitoring populations over a longer period whilst continuing to expose them to predation. During this time, the population would need to persist and adapt, including with recruitment of predator-resistant individuals to the population. Our study was not long enough to produce conclusive evidence about the lower threshold of the goldilocks zone. We were not able to test for any phenotypic or behavioural changes post-release. However, clearly some bettongs in our study survived a long time (> 1 year) while others succumbed to predation very quickly. This disparity suggests that selection of bettongs indeed took place (i.e. that we are showing a pattern that is necessary for selection to occur). More research is needed to answer whether this predation level is low enough to allow for survival whilst still conferring fitness advantages that enable continued population persistence. In Moseby et al. (2018), the authors investigated whether low levels of predation by cats would drive selection in the burrowing bettong. They found that physical and behavioural traits measured before release were not predictors of survival and concluded that the predation pressure they established may have been too low to drive strong selection over a short period. Despite this conclusion, Moseby et al. (2018) did observe a significant change in hind foot length in the male population of predator-exposed bettongs. Further, West et al. (2018) observed behavioural changes in a populations of bettongs exposed to predation. We observed that larger bettongs were more likely to survive than smaller individuals. Further studies should investigate whether the observed size differential or any hidden behavioural or phenotypic trait confers increased predator resistance over the long term.

The Goldilocks Zone will function as intended only if selection results in evolution. That is, predator-resistant traits need to be conferred to young to increase population-level predator resistance. Although we observed female bettongs with pouch young and young at foot, we saw no evidence of recruitment to the population of predator-resistant bettongs (though we recognize that this result may be an artifact of the small sample size of females and the relatively short period of the study). Predators often target the juveniles, the weak and the sick (Genovart et al. 2010). The fact that larger bettongs (i.e.,  $\geq 1.5$  kg) in this study survived better, raises the possibility that younger (and, therefore, smaller) bettongs may succumb to predators before becoming established adults (assuming it is weight that confers predator resistance, and not some associated trait). This survival differential implies that there is a chance that the upper threshold below which fully grown adults survive could, in the long term, preclude the persistence of a population, simply because young do not survive to adulthood. However, our study could not prove or disprove this survival

differential and only with further trials, including more reintroductions and a continued effort to maintain fox activity within the Goldilocks Zone, can we establish the thresholds in which populations can persist.

One of the key challenges for the Goldilocks Zone is maintaining the required level of predation and containing intermittent spikes of predation above the upper threshold. Challenges such as landscape-scale fox activity and adaptation of fox populations to control regimes, make maintaining the level more difficult through time. In our study, after an initial knockdown in May 2015, fox numbers remained low for 2 years until May 2017. After this time, despite continuation of the intensive ejector and baiting regime, fox numbers reached an undesirable level and ultimately prevented the long-term persistence of the bet-tong population. A further challenge is that fox numbers fluctuate throughout the year due to juvenile emergence and dispersal (Saunders et al. 1995), though our data suggest that this fluctuation does not happen every year. Managing these potential spikes requires an effective monitoring network that can react to increases of fox numbers in enough time to avoid breaching the upper threshold of predation (i.e., adaptive management).

Our work adds to a body of literature exploring the potential of harnessing evolutionary principles to combat animal management challenges. Animal management can have unintended evolutionary consequences (Shefferson et al. 2018). Refuge naïveté is one of them, and there has been important recent work exploring the challenges and solutions that prey naïveté poses for reintroductions (Moseby et al. 2016, 2018; Jolly et al. 2018; Steindler et al. 2018; West et al. 2018).

The unintended consequences of predator management are also of concern. When attempting to control predator species, managers may inadvertently select for resistance to control, making the problem worse in the longer term (Shefferson et al. 2018). Hunting and fishing is known to drive selection (Allendorf and Hard 2009). Indeed, human predation is considered one of the most rapid drivers of selection, outpacing many other more ‘natural’ drivers (Darimont et al. 2009).

We should expect fox control practices to result in selection pressures that make fox control more difficult over the long term. We know from previous studies that lethal control of foxes rarely results in complete eradication (Thomson et al. 2000), and is usually followed by a reinvasion of foxes from the surrounding landscape (Gentle et al. 2007; Saunders et al. 2010). Foxes are generally territorial (White et al. 1996) so new foxes fill the gap in the landscape caused by the removal of an individual fox (Newsome et al. 2014). Foxes persist in Australia, despite decades of control practices. Their persistence suggests control measures have been largely unsuccessful at the broad scale, and potentially created selection pressures that have made fox control more difficult. Rapid adaptation of the red fox has been demonstrated in urban (Parsons et al. 2020) and captive populations (Dugatkin et al. 2017). For researchers measuring fox population density, selection pressure may also cause responses to baits to change, meaning that measures of abundance using bait take become unreliable. For example, fox populations in a rangeland in Western Australia demonstrated compensatory responses to baiting by increasing their ovulation rates, implantation rates and litter sizes (Marlow et al. 2016).

Purposefully controlling predators within the levels required to maintain a Goldilocks Zone is almost certain to result in selection. By allowing a small number of individual foxes to remain, our control actions may have inadvertently selected for control-resistant foxes. For example, in our control program, there was a divergence of ground bait take and ejector activation from May 2017 (Fig. 3a). Ground bait take increased while ejector activation stayed at almost the same level. This result could indicate that ejectors became less effective through time. If we assume that foxes that activate ejectors are killed quickly and



efficiently (Fleming et al. 2006), it could indicate a strong selective force leading to a landscape with foxes that are ejector averse. We did not observe in our data selection for ground bait-averse foxes, but over a longer period it is possible that ground bait aversion too could arise. Ground baits are less effective at killing foxes, and could elicit bait aversion in cases where a fox is partially poisoned, but survives (Allsop et al. 2017). Our results suggest the possibility that fox control measures could lead to selection for foxes that are hard to control with ejectors and ground baits, especially if bait-aversion traits are passed on to their young. The evolutionary consequences of controlling predators at a low level are unclear, and impossible to determine over the timescale of this study and should be considered in future studies.

A possible avenue to explore that overcomes the unintended consequences of lethal control is to reduce predation whilst predators remain in the landscape (Shivik et al. 2003). In particular, non-lethal techniques that exploit known behaviors offer promise, such as using odors to manipulate fox foraging and predation behaviors (Leo et al. 2015). This tactic might reduce predation pressure within the levels required for selection of predator-resistant prey (i.e., the Goldilocks Zone) without creating the strong selective forces associated with lethal control. We acknowledge, however, that imposing any manipulation on a population or system will inevitably result in selection. Understanding the adaptive responses in these systems will be integral to understanding how predators will respond in the long term.

We recognize that we did not target cats when reducing predation pressure on bettongs at the LCC, although some cats were caught by managers during the project. Bettongs and feral cats have co-existed in Tasmania since the early 1800s (Abbott 2008) without resulting in the extinction of the former. That said, cats are known to prey upon bettongs, and have been implicated in population declines and crashes in several species of Australian mammals (Legge et al. 2017; Radford et al. 2018), including a closely related species of bettong (Bannister et al. 2016). Cats have been used recently to test predator exposure as a tool to select against predator naïveté in the burrowing bettong (Moseby et al. 2018; Saxon-Mills et al. 2018; West et al. 2018). Cats were much less prevalent than foxes in the LCC (camera captures: foxes=450, cats=89). Further, our results demonstrated a direct correlation between bettongs and fox numbers, and managers judged predation by foxes to be the cause in a large amount of bettong deaths. No deaths were attributed to cats (Table S2), indicating that foxes were the main predators of bettongs in the area. Nevertheless, it is possible that cats may have contributed to background predation levels. Further, we advise caution because controlling foxes can result in changes in cat behaviors and populations which may result in increased impacts of cats in the long term (Marlow et al. 2015a; Newsome et al. 2019). Cats, therefore, should still be considered potentially influential predators in future studies such as ours.

We recognize that there is a large amount of uncertainty driven by the low number of bettongs used in our study. With the low power we have in our study, selection is uncertain and there is a chance that the bettongs that survived the longest may have done so randomly. In undertaking critical research on threatened species to enable reintroduction success in the long-term, trials need to be parsimonious in the number of founders used to yield the maximum learning (Costello et al. 2016; Wilson et al. 2020) (indeed, this parsimony is a requirement for university ethics committees). Such studies are inevitably characterized by low replication and control (Kemp et al. 2015), but this pragmatic approach, as we have used here, can reveal valuable insights despite uncertainties and low numbers, that can inform further adaptive trials and ultimately full reintroduction (Batson et al. 2015; Kemp et al. 2015; Wilson et al. 2020).

## Conclusions

We discuss the Goldilocks Zone of predation in the context of CWR mammal reintroductions beyond-the-fence in Australia. CWR mammal extinctions in Australia make up a substantial component of biodiversity loss worldwide (Johnson and Isaac 2009; Radford et al. 2018), so we see potential for our concept to contribute to mitigating this loss. The Goldilocks Zone concept is simple and easy to understand. It could complement work already being done on using evolutionary principles in reintroductions of CWR mammals (Bannister et al. 2016; Moseby et al. 2016, 2018; West et al. 2018), and potentially guide future work in this area.

There is still some way to go to establish self-sustaining populations beyond-the-fence for Australian CWR mammals. More research is needed to determine whether selection in the presence of exotic predators results in recruitment of predator-resistant CWR mammals in subsequent generations. More work should also be done to determine the traits that increase the chance of survival of CWR mammals in the presence of exotic predators. This work would allow managers to increase their reintroduction success beyond-the-fence, while allowing them to be parsimonious in the number founders needed. The Goldilocks Zone concept, introduced and demonstrated here, offers a potential pathway for the co-existence of native CWR mammals and exotic predators in Australia.

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**Data availability** Data presented in this manuscript are available upon reasonable request.

**Code availability** R code used in the analysis in this manuscript will be made available on reasonable request.

## Declarations

**Conflict of interest** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**Ethical approval** This project was covered by ANU Animal Ethics and Experimentation Committee Protocol A2015/73.

**Informed consent** All authors gave final approval for publication and agree to be accountable for its content.

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