Designer prey: Can controlled predation accelerate selection for anti-predator traits in naïve populations?

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ARTICLE INFO

ABSTRACT

Prey naïveté is thought to be a significant factor contributing to the failure of native prey to re-establish in the presence of introduced predators. We tested whether exposing naïve prey to low levels of *in situ* predation pressure from introduced predators could cause accelerated selection for certain physical or behaviour traits. Such selection could improve the chance of future co-existence between introduced predators and native prey. In 2014, we reintroduced 352 burrowing bettongs (*Bettongia lesueur*) into a 26 km^2 fenced paddock where predation levels could be carefully controlled. Four feral cats (*Felis catus*) were introduced to the paddock several months after bettong reintroduction and predation events were subsequently recorded. We measured a suite of physical and behavioural traits on the bettongs prior to release and compared these between individuals that survived or were assumed to have died. Population level parameters were also compared between the reintroduced population and the predator-free source population. No *a priori* measured physical or behavioural traits were significant predictors of individual survival after release and the high survival rate of radio-collared bettongs and the positive population growth rate suggests that the predation pressure from the introduced feral cats may not have been sufficiently high to cause strong selection over a short time period. However, population level comparisons found cat-exposed male bettongs had significantly longer hind feet than the source population at 18–22 months after release. Hind foot length was consistently longer in both older released animals and younger recruits and thus may be an indicator of selection and/or phenotypic change in response to the presence of predators. Our study suggests that predation may cause phenotypic change over short time periods but that higher cat predation pressure may be required to enable the benefits of accelerated natural selection to be adequately assessed.

1. Introduction

Introduced predators have caused the extinction of native prey throughout the world and continue to cause significant impacts to populations of native wildlife (Johnson, 2006; Moseby et al., 2011; Towns et al., 2011). Introduced mammals, including cats (*Felis catus*) and red foxes (*Vulpes vulpes*), have contributed to the extinction of > 20 species of mammals weighing < 5 kg (Johnson, 2006) and numerous species of birds and lizards (King, 1984; Towns et al., 2001) respectively. The impacts of introduced predators are widespread and not confined to islands; significant faunal declines have been recorded in California after the introductions of the red fox (Lewis et al., 1999). The risk of future predator incursions is high globally because an increasing human population is likely to cause more inadvertent and deliberate introductions of predators into populations of unprepared prey.

Exotic predators can have higher impacts on prey than native predators (Paolucci et al., 2013) due, in part, to evolutionary naïveté which is a lack of co-evolution between introduced predators and native prey (Griffin et al., 2000). Conservation programs attempt to reduce the impact of introduced predators though methods such as predator exclusion *via* fencing, direct control and eradication. Control techniques such as poisoning, biological control, and shooting/trapping are problematic, the methods may become less effective over time due to selection (Allen et al., 1996; Kohn et al., 2000; Warburton and Drew, 1994), results can be short-lived (Côté and Sutherland, 1997) and the on-going nature of control requires long-term funding commitments. Fencing has recently become a popular method for protecting native prey from predators such as feral cats and foxes and effectively isolates native prey from introduced predators. Unfortunately, complete removal of predation pressure can lead to significant and rapid loss of

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prey anti-predator behaviour through relaxed selection (Blumstein, 2006; Lahti et al., 2009). This isolation, whilst a highly effective short term conservation tool, exacerbates the problem of prey naïveté as evidenced by the severely compromised predator avoidance strategies of individuals from some predator-free areas (Biggins et al., 1999; McLean et al., 2000). Additionally, whilst introduced predators have been eradicated from small islands (Nogales et al., 2004) they have not been eradicated from any continents or countries suggesting that introduced predators are likely to remain in the environment for the foreseeable future.

A potentially more effective way of achieving the long-term co-existence of native prey and introduced predators may be to improve the anti-predator responses of native prey. *In situ* predator exposure is a technique where native prey are exposed to introduced predators at low densities over long time periods to improve behavioural responses of prey through learning and natural selection (Moseby et al., 2015a, 2015b). Under these conditions some prey will be attacked and killed but others may survive direct encounters or learn through their own and others' experiences. This accelerated selection may facilitate the evolution of prey populations that can tolerate and co-exist with introduced predators. Research already suggests that previously naïve survivors can modify their behaviour after direct or vicarious experiences with predators (Berger et al., 2001). Human activity and biological invasions can drive rapid phenotypic change (Darimont et al., 2009; Phillips and Shine, 2004) through the processes of natural selection and phenotypic plasticity (Hendry et al., 2008; Kohn et al., 2000).

For *in situ* predator exposure to be successful, it must either target ontogenetic naïveté through improvements in individual learning and/or evolutionary naïveté through natural selection at the population level. Demonstrating selection would require differential survival of individual prey based on behavioural or physical traits. Population changes may also occur that are unrelated to selection. For example, non-lethal effects of predation can result in phenotypic changes such as shifts in the expression of physiological traits and behaviour (Creel and Christianson, 2008; Banks et al., 1999). We tested whether *in situ* predator exposure could generate a response to selection by exposing a reintroduced population of naïve prey to controlled densities of exotic predators. Physical and behavioural traits were measured for reintroduced burrowing bettongs (*Bettongia lesueur*) prior to release and compared between individuals that survived or were assumed to have died. Population level parameters were also compared in the reintroduced population before and after release and to a control population where predators were absent. In order to differentiate between phenotypic plasticity and selection, we measured changes in traits within the reintroduced population as well as in animals recruited into the population after release. We chose to use the feral cat as the introduced predator species because it has contributed to the extinction and previous reintroduction failure of bettongs (Moseby et al., 2011) and a range of other threatened mammal species (Dickman, 1996; Woinarski et al., 2014). Unlike red foxes, feral cats are difficult to control using broadscale control methods and other techniques are urgently needed to reduce their impacts. Foxes can also surplus kill and cause rapid population decline at even low densities (Short and Turner, 2000) which was not suited to maintaining and controlling a low level of sustained predation pressure. Results were used to test whether *in situ* predation could cause accelerated selection for physical or behavioural traits and thus may be a useful tool for enabling future co-existence of native prey and exotic predators.

2. Methods

2.1. Study site

This study was conducted at the Arid Recovery Reserve in northern South Australia (Fig. 1). The reserve comprises a 123 km^2 area which has been fenced to exclude introduced rabbits (*Oryctolagus cuniculus*), cats and foxes. Bettongs were moved from one section of the reserve where foxes and cats have been eradicated and excluded since 1998 (Source) into two other sections of the reserve; a cat-free section (Control) and another section of the reserve where rabbits were still present and cats were later added (Cat Treatment, Fig. 1). The 26 km^2 Cat Treatment paddock is surrounded by a mesh fence (1.4–1.8 m high) with an external floppy overhang to prevent access by feral cats and foxes.

The Source, Control and Cat Treatment paddocks were located within a 10 km radius (Fig. 1). The landforms in each paddock were characterized by clay interdunal swales interspersed with longitudinal orange sand dunes. Vegetation of the inter-dunal swales was dominated by chenopod shrubs (*Atriplex* spp. and *Maireana* spp.). Vegetation on the dunes was dominated by the shrubs *Acacia aneura*, *Acacia ligulata* and *Dodonaea viscosa*, and annual grasses and forbs. The proportion of each major habitat type was similar between the three areas and their close proximity ensured minimal variation in habitat or climatic features.

All three paddocks have a recent history of occupation by bettongs; bettongs have been present in the Source paddock since their reintroduction in 1999, in the Control section since their reintroduction in 2002 and bettongs have been present in the Cat Treatment paddock for three years from 2009 until their extinction in 2011 from a fox incursion. The Cat Treatment paddock also contained rabbits at low population densities. The only native predator of the bettong in the region is the wedge-tailed eagle which was present and able to access all three treatments.

Rainfall is erratic, failing to reach the long-term average of 160 mm in 60% of years. Bettongs were moved towards the end of 2014 which was a below average rainfall year following two successive dry years (2012-104 mm and 2013-131 mm, 2014-100 mm). Rainfall reached the average in 2015 (154 mm) and was above average in 2016 (266 mm). Four threatened species (greater bilbies (*Macrotis lagotis*), burrowing bettongs, western barred bandicoots (*Perameles bougainville*) and stick-nest rats (*Leporillus conditor*)) have been previously reintroduced to other sections of the Arid Recovery Reserve including the Source and Control area (Moseby et al., 2011) but were not present in the Cat Treatment at the time of this study.

2.2. Study species

Burrowing bettongs are a medium-sized, macropodid marsupial that live communally in burrows. They weigh approximately 1.6 kg and formerly roamed over > 60% of Australia (Woinarski et al., 2014). They have declined by > 90% since European settlement and are now found naturally only on three offshore islands in Western Australia (Short and Turner, 2000). Their decline is thought to have been caused by predation from introduced foxes and cats as well as habitat degradation and possibly disease. Burrowing bettongs have been successfully reintroduced to fenced mainland sanctuaries and islands where cats and foxes are absent but several attempts to release them into areas where introduced cats and foxes are present have failed due to predation (Bannister et al., 2016; Moseby et al., 2011).

2.3. Reintroductions

Between October and December 2014, a total of 352 burrowing bettongs (147 females and 205 males) were reintroduced into the Cat Treatment from the Source area of the Arid Recovery Reserve where rabbits, cats and foxes were absent. At the same time, 10 bettongs were also moved into the Control area to control for any impact of translocation on bettong survival. Ideally, the Control area would have comprised unoccupied predator-free habitat but there were no other predator-free areas available in the study area where bettongs were absent. Control and Cat Treatment areas needed to be in close proximity to
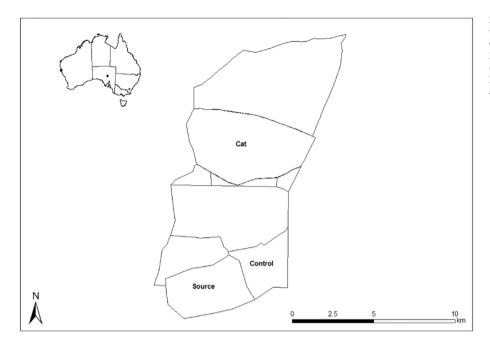
Fig. 1. Map of Arid Recovery Reserve showing location of the Source (Main Expansion), Control (First Expansion) and Cat-exposed (Red Lake Expansion) treatments. The Arid Recovery Reserve is comprised of 6 fenced compartments. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

minimise habitat and rainfall differences. To compensate for this we removed 22 bettongs from a dune within the Control area to create an unoccupied habitat for the translocated bettongs to establish within. These bettongs were moved > 5 km away to other fenced areas of the reserve to prevent them returning. None of the moved bettongs were recaptured at the removal site but some were recaptured during routine monitoring in other parts of the reserve.

Bettongs were captured at warrens in cage traps baited with peanut butter and rolled oats. Each trap had a hessian sack placed over the back half of the trap to reduce stress on trapped animals. Traps were checked between 2 and 6 h after dark. Bettongs with large pouch young (> 80 mm crown to rump) were not moved and immediately released at point of capture. All bettongs were released at the same point in the Cat Treatment and all releases were during darkness.

We trapped, marked and fitted VHF radio collars (25 g, Sirtrack Ltd. with mortality sensors) to 26 burrowing bettongs in the Cat Treatment paddock, 23 were radio-collared prior to the move and three additional bettongs were collared 8 months after the move to increase the sample size (August 2015). Ten bettongs were radio-collared prior to their move into the Control area. All collared bettongs were captured and collared at their warrens 1–2 months before the reintroduction and then trapped again on the night of translocation.

2.4. Cat introduction

No cats were present in the Control or Source treatments throughout the study. At the start of the release into the Cat Treatment in October 2014, camera trap, spotlighting and spoor data indicated that there was one cat of unknown sex (suspected female from remote camera images). Five additional cats (4 males and 1 female) were added to the Cat Treatment between 6 and 8 months after bettong release and their continued presence within the paddock was monitored using radio-tracking, spoor counts and camera trap grids (20 Bushnell Cameras set along vehicle tracks and checked monthly). Cats were given a unique ear tag placement to enable identification on camera and male cats were sterilised to prevent breeding before being added to the exclosure. Large male cats were targeted for introduction because previous research has suggested that large male cats are disproportionately responsible for predation on threatened species (Moseby et al., 2015a, 2015b). Cats in the study region typically weigh < 4 kg; males average 3.9 kg, and females average 2.8 kg (Read and Bowen, 2001).

2.5. Physical and behavioural traits

We recorded a range of behavioural and physical traits for all translocated bettongs and compared them between bettongs that later died and survived. We recorded specific bettong behaviours in response to trapping because prior work demonstrated that some of these are individually distinctive, repeatable, and correlated with natural anti-predator behaviour (West et al., 2017). Thus, we dichotomously scored whether animals moved in the trap, made noise, moved immediately from the trap into a capture bag when the door of the trap was opened and whether they moved in an agitated manner once they were secured in the bag. We then summed these scores and subtracted from a total score of 4 to give a trap docility score where 0 = non-docile and 4 = docile. We also recorded the latency (seconds) for each bettong to leave the trap and enter the catch bag.

All trapped bettongs were weighed, sexed, measured to the nearest mm (hind foot length (pes), testes width and head length), checked for body condition (score of 1 to 4, 1 being poor and 4 excellent) and reproductive status, given a unique ear tag and released into the Cat Treatment on the same night of capture. A body condition index was calculated using the cube root of body mass divided by pes length (Short and Turner, 2000). We also recorded the crown to rump length of pouch young. All measurements were made by the same, trained personnel to reduce inter-observer errors (RW, KM).

2.6. Individual survival

Survival of individual bettongs after release was measured using both radiocollared bettongs and recapture of released individuals. Survival checks for radio-collared bettongs in the Control and Cat Treatment were conducted weekly for 20 months post-reintroduction. Any mortality signals were located and carcasses and/or collars retrieved. The location of the collar and/or carcass was recorded as above ground or down a warren as previous cat predation events on bettongs have all been recorded above ground (Moseby et al., 2011; pers obs). Collars and bodies were swabbed for predator DNA analysis using buffer and nylon swabs and analysed by Ecogene (Canberra, ACT). Radio-collars and carcasses were also inspected to determine the cause of mortality.

In April 2016, 18 months after bettong releases into the Cat Treatment, an intensive cage trapping session was implemented to

identify survivors. We set 140 Sheffield cage traps for four nights (total trap nights 560), evenly spaced along the 35 km road network within the Cat Treatment. Traps were cleared each morning at dawn and animals were identified using eartags, weighed, measured and checked for body and reproductive condition. To increase trapping effort we also trapped at 10 warrens in June 2016 (total trap nights 60) and 24 warrens in September 2016 (total trap nights 174) located away from the roads within the Cat Treatment to maximise the chances of capturing individuals not recorded in the April session. We also sampled the physical characteristics of the population in the Source area at a similar time by conducting cage trapping in August 2016 in the main expansion of the reserve. We set 160 cage traps along the road network for 4 nights (total trap nights 640).

To determine if there were traits associated with survival, within the Cat Treatment we compared the physical characteristics and behavioural traits of known survivors with assumed fatalities (animals not recaptured in any subsequent session since release). We then also compared these traits only in radio-collared bettongs in the Cat Treatment where survival was known with certainty (9 deaths out of 26 radio collared bettongs).

2.7. Population changes

To determine if the distribution of morphological traits in the Cat Treatment population had changed in the presence of cats we compared physical traits of adult bettongs (> 950 g, Tyndale-Biscoe, 1968) in the Source population at the time of reintroduction (Source Before) with bettongs captured in the Cat Treatment (Cat After) and Source population (Source After) 18 and 22 months later respectively. To separate out any age-related effects, any physical traits that were significantly different between bettongs in the Cat After and both Source Before and Source After treatments were further investigated by dividing the Cat After bettongs into cohorts; survivors (bettongs that were originally released animals) and recruits (bettongs born since release). These two cohorts were compared with Source After and Source Before treatments to determine if differences were age-related, due to natural selection or due to phenotypic plasticity.

2.8. Statistical analyses

We examined differences in survival between radio collared Cat Treatment and Control bettongs using Kaplan Meier survival analyses in SPSS (IBM statistics v23). We compared survival distributions over two time periods, the first 52 weeks after release and across the entire study period.

For the individual survival comparisons, we fitted generalised linear models with a binomial distribution in package lme4 (Bates et al., 2014) in R version 3.3.1 to test whether survival of bettongs in the cat treatment was predicted by the covariates of sex, weight, pes length, body condition index (cube root of pes divided by weight), condition score, trap docility score and latency to leave the trap. We standardised all covariates to a mean of zero. Covariates were examined for co-linearity using Pearson correlation coefficients and significantly co-linear values $r > 0.7$ were excluded from the same model. To examine the relative significance of each predictor variable within the model we used 'drop1' to conduct single term deletions of each fixed effect from the model and compared the AIC of the reduced model to a full model using Chi-square tests. We also fitted the same models to the dataset for collared bettongs in the cat treatment where fate was known for each individual.

For the population level comparisons, we fitted univariate general linear models in SPSS (IBM Statistics v23) to test for significant differences in physical traits between three treatment groups (Source Before, Source After, Cat After) using Tukey's LSD post-hoc tests. We examined body mass, body condition index, pes length, pouch young size and testes width. In each linear model we included sex as a fixed

factor and where sex was significant we ran separate models for each sex. Where post-hoc tests revealed significant differences between Cat After and both Source Before and Source After we divided the bettongs in the Cat After treatment into cohorts to distinguish between age effects and selection. In the Cat After treatment we were able to distinguish individuals as Cat Recruits (born since translocation) and Cat Survivors (original release animals) based on the presence of ear tags. Unfortunately, we were unable to divide Source bettongs into cohorts because the majority of animals were untagged when we trapped at 22 months after animals had been removed for translocation into the Cat Treatment. We fitted general linear models to test the effect of group (Cat Recruit, Cat Survivor, Source Before, Source After) on each characteristic for which Cat Treatment and Source Before and Source After were significantly different. If Cat Recruits and Cat Survivors did not differ from each other but were both significantly different to Source Before and Source After animals then this would indicate selection for a particular trait. In all cases we set our alpha to 0.05. We also compared sex ratios and the proportion of females with pouch young in each treatment using contingency tables.

3. Results

3.1. Mortalities

Twelve of the 36 radio collared bettongs (33%) died over the 18-month study period (Table 1). Previous Arid Recovery trapping data suggests bettongs can survive for up to 8 years after first capture but animals are more commonly re-trapped over periods of 3–4 years (Arid Recovery unpublished data). Another study on wild burrowing bettongs found the species can be retrapped for periods in excess of three years (Short and Turner, 2000). There was no statistical difference in the proportion of bettong deaths in each treatment with 3 of the 10 collared bettongs in the control area dying and 9 of 26 in the cat treatment (Fisher Exact test p = 0.716). There was a difference in the types of mortalities between the two treatments, with more surface mortalities in the cat treatment and more bettong mortalities within warrens in the control treatment (Table 1). Collared bettongs that died in their burrows were dug up and inspected for cause of death. These individuals were intact and in various stages of decomposition. No sign of predation was recorded consistent with personal observations that bettongs often die in their burrow when deaths are recorded in predator-free environments (K. Moseby pers. obs, 2016). Conversely, bettongs found dead on the surface in the cat treatment were all attributed to cat predation due to the location of the collar and carcass and/or canine teeth marks found on the collar, DNA analysis, signs of struggle and/or fur and other remains. Two of the surface mortalities in the cat treatment tested positive for cat DNA. In both cases these collars or carcasses were pulled under bushes, a common tactic used by feral cats when consuming their prey (unpublished observations). The bettong found dead on the surface in the control treatment was attributed to predation by a wedge-tailed eagle (*Aquila audax*) because it was found out in the open, the brain had been eaten and the body stripped into pieces. Despite more bettongs dying on the surface in the cat treatment, when the proportion of radiocollared bettongs dying on the surface was compared between control and cat treatments using a Fisher Exact test,

Table 1
Summary of mortalities in cat and control treatment. 'Lost' signals refers to collars that were not heard after release, bodies never retrieved but animals never re-caught so assumed died.

Treatment	# Collars	Mortalities total	Warren mortalities	Surface mortalities	Lost signals
Control	10	3	2	1	0
Cat	26	9	3	4	2

there was no significant difference (p = 0.546).

Although there was a trend towards lower survival in the cat treatment (Fig. 2), there was no significant difference in survival distributions of collared bettongs between treatments in the first 12 months (52 weeks) post-release (X^2 = 1.749, df = 1, p = 0.186) or across the entire study period (X^2 = 0.539, df = 1, p = 0.463) (Fig. 1). When only surface mortalities were included in the Kaplan Meier analysis there was still no significant difference in survival distributions between the two treatments (X^2 = 1.191, df = 1, p = 0.275).

3.2. Individual survival

In April 2016 we caught 211 bettongs (129 male, 82 female) of which 102 were originally translocated animals and 109 were new recruits since translocation. Warren trapping in June 2016 identified an additional 10 original translocation animals (out of 30 total captures) that had not been captured in the April trapping session along roads. Warren trapping in September 2016 identified an additional 6 originally translocated bettongs (out of 96 total captures). The proportion of originally released animals captured for the first time after release declined over the three trapping sessions (48% April, 33% June, 6% September) suggesting that we had recaptured a significant portion of the released individuals that had survived since translocation. For the purposes of the survival analysis we therefore assumed that of the 352 bettongs translocated, 118 had survived and 234 bettongs had died.

There was significant co-linearity between the covariates of weight and body condition index so we tested two models, one with weight and the other with body condition index. We found no significant predictors of individual survival for the 352 translocated bettongs using either model (Table 2, only model outputs with weight are shown). Drop 1 tests did not reveal improvements in model fit through the deletion of any single covariate.

We also tested survival data using only bettongs in the cat treatment that were radiocollared (n = 25) and where the survival of individuals was unequivocal. However, due to the small number of observations for collared bettongs (n = 25), we ran two separate models with three covariates in each (model 1 – weight, pes, sex; model 2 – condition, trap score, latency to leave trap) to avoid over-factoring. There were no

Table 2
Results of generalised linear model to compare four physical characteristics and two behavioural scores with survival of 352 bettongs translocated into a paddock with feral cats.

	Estimate	Standard error	p value
Intercept	− 0.537	0.175	0.002
Sex (male)	− 0.271	0.234	0.246
Weight	0.130	0.167	0.433
Pes	− 0.021	0.130	0.872
Condition score	− 0.141	0.152	0.352
Trap docility score	0.170	0.118	0.151
Latency to leave trap	− 0.069	0.234	0.247

significant predictors of survival. Drop 1 tests did not improve model fit.

3.3. Population changes

We first compared physical characteristics of adult bettongs in three groups – Source Before, Source After and Cat After (Table 4). Significant differences between Cat After and both Source Before and Source After were investigated because these would suggest a significant change in the physical characteristics of the bettong population exposed to cats.

Pes length and BCI were the only variables that were significantly different between bettongs in the Cat Treatment and the source population both before and after bettong removal. Within the cat treatment, bettong body condition was lower and male bettongs had longer pes measurements when compared with the source population before and after translocation. There was a significant effect of treatment (F = 7.361, df = 2, p = 0.001) and sex (F = 35.02, df = 1, p < 0.001) on pes length, so males and females were analysed separately. Whilst there was no overall effect of treatment on female pes length (F = 0.620, df = 2, p = 0.539), males in the cat treatment had significantly larger pes measurements than either Source Before (mean difference = 1.45 ± 0.37 se, p < 0.0001) or Source After bettongs (mean difference = 1.81 ± 0.40 se, p < 0.0001). There was no difference in the pes lengths in the source population before and after animals were removed (mean difference = 0.35 ± 0.36se,

Table 3
Results of two generalised linear models to compare four physical characteristics and two behavioural scores with survival of radiocollared bettongs in the cat treatment.

	Estimate	Standard error	p value
Model 1			
Intercept	1.638	0.836	0.050
Sex (male)	− 1.369	1.014	0.177
Weight	− 0.378	0.456	0.407
Pes	0.429	0.508	0.398
Model 2			
Intercept	0.801	0.448	0.074
Condition score	− 0.034	0.450	0.939
Trap docility	0.552	0.548	0.314
Latency to leave trap	0.177	0.478	0.711

$p = 0.327$). There was a significant effect of treatment on Body Condition Index ($F = 52.54$, $df = 1$, $p < 0.0001$) but not sex ($F = 3.24$, $df = 1$, $p = 0.72$). Bettong BCIs had decreased in the cat treatment compared to before they were moved (Cat After *vs* Source Before, mean difference = − 0.59 ± 0.06 se, $p < 0.0001$) and were lower than the bettongs in the Source population at the same time period (Source Before *vs* Source After, mean difference = − 0.46 ± 0.06 se, $p < 0.0001$) (Table 3). Although head length was only measured in bettongs in the Cat After and Source After populations after release, there was a significant difference in head length between treatments ($F = 5.74$, $df = 2$, $p = 0.017$) and sexes ($F = 7.216$, $df = 1$, $p = 0.008$). When head length was analysed separately for males and females there was a significant difference in head length in female bettongs ($F = 12.51$, $df = 1$, $p = 0.001$) but not males ($F = 0.058$, $df = 1$, $p = 0.811$). Female head lengths in the Cat After treatment were significantly smaller (average 72.9 ± 7.81 se) than the Source After population at the same time period (average 76.4 ± .5.05 se).

In order to test whether these differences may be age related or driven by selection, the cat-exposed bettongs (Cat After) were divided into cohorts based on whether they were original release animals (Cat Survivors) or adult animals recruited into the population since translocation (Cat Recruits). Significant differences between both Cat Survivors and Cat Recruits compared with Source animals at the same time (18–22 months after exposure) could suggest selection is occurring whilst significant differences between only Cat Recruits and Source After animals may indicate age-related effects. When BCI, female head length and male pes were compared between Cat Recruits, Cat Survivors and Source Before and Source After treatments, Tukey *post hoc* tests on significant treatment effects indicated that only male pes was significantly longer in both Cat Recruits and Cat Survivors compared with Source Before and After animals (treatment effect $F = 8.104$, $df = 3$, $p < 0.001$). Female head length ($F = 8.094$, $df = 3$, $p < 0.001$) and BCI ($F = 46.18$, $df = 3$, $p < 0.001$) were

significantly different between treatments but Tukey *Post Hoc* tests revealed that only the Cat Recruits cohort was significantly different to Source Before and Source After animals, thus indicating a likely age effect (Table 5).

Other variables differed significantly between treatments but did not differ between Cat After and Source After populations suggesting that differences were due to changes in seasonal conditions between the time of release and the time of resampling 18–22 months later.

There was a significant effect of treatment ($F = 46.68$, $df = 2$, $p < 0.0001$) and sex ($F = 4.43$, $df = 2$, $p = 0.12$) on weight. We therefore conducted separate analyses for males and females to compare the effect of treatment. Males and females were both significantly heavier in the source population at the time of reintroduction (Source Before) than either the cat or source population after reintroduction (males $F = 40.22$, $df = 2$, $p < 0.0001$, females $F = 13.41$, $df = 2$, $p < 0.0001$). There was no difference in weight between Cat After and Source After populations. Similarly, male testes size differed between treatments ($F = 7.54$, $df = 2$, $p = 0.001$) but only between the source population at the time of reintroduction and both cat after and source after.

There was no effect of treatment on pouch young size (Table 4, $F = 0.279$, $df = 1$, $p = 0.598$) and the proportion of adult females carrying pouch young was the same in both the cat and source population 18–22 months after reintroduction.

4. Discussion

Despite evidence of cat predation on burrowing bettongs, we detected no physical or behavioural traits that were significantly associated with their individual survival after being introduced into a large paddock with cats. Survival of radiocollared individuals in the Cat Treatment paddock was high and not significantly different from survival in the Control area. However, when we compared the physical traits of the bettong population exposed to cats with that of the source population over the same time period, some significant differences in physical characteristics were recorded.

Cat densities within the Cat Treatment paddock (0.038–0.15 cats/km²) were within the range of cat densities (range 0.01–2.4 cats/km2, average 0.18 cats/km²) reported in the wild in arid Australia during dry conditions by Legge et al. (2017). Additionally, a removal experiment conducted at Arid Recovery adjacent to the study site suggested a natural feral cat density of 0.14 cats/km² (Legge et al., 2017). Although these densities are sufficient to cause the failure of previous threatened species reintroductions in the region (Moseby et al., 2011), predation pressure from cats may not have been sufficiently high to enable us to detect correlates related to individual survival. Evidence to support this hypothesis comes from the similar survival rates of radiocollared bettongs in the Cat and Control treatments despite the absence of introduced predators from the Control area. Although we introduced

Table 4
Comparison of physical characteristics (mean ± standard deviation) and reproductive output of adult bettongs (> 950 g) in the three treatments; Source Before (no cat exposure), Source After (22 months after animals were removed for translocation into the cat-exposed treatment) and Cat After (18 months after bettongs were translocated to the cat-exposed treatment). BCI = body condition index. Brackets indicate sample size if different from n.

	n	Sex	Mean weight (g)	Body condition index	Head length (mm)	Pes (mm)	Females with pouch young (%)	Average pouch young size (mm)	Testes size (mm)
Source Before	349	all	1550 ± 268	5.00 ± 0.81	Not recorded	103.2 ± 3.1			
	204	M	1588 ± 282	5.10 ± 0.86		103.6 ± 3.0			19.61 ± 4.26 (203)
	145	F	1498 ± 240	4.87 ± 0.74		102.5 ± 3.1	1	30 (1)	
Cat After	229	All	1379 ± 179	4.42 ± 0.58 (228)	75.08 ± 8.39 (151)	104.2 ± 3.8			
	139	M	1381 ± 165	4.38 ± 0.52	76.56 ± 8.50 (90)	105.1 ± 3.4			21.00 ± 0.26
	90	F	1377 ± 200	4.47 ± 0.67 (89)	72.90 ± 7.81 (61)	102.8 ± 4.0	81	45.7 ± 2.78 (76)	
Source After	262	All	1405 ± 192	4.54 ± 0.61 (259)	76.35 ± 5.01 (259)	102.9 ± 3.5 (259)			
	149	M	1425 ± 193	4.59 ± 0.63 (147)	76.34 ± 5.47 (147)	103.3 ± 3.7 (147)			20.83 ± 0.29 (144)
	113	F	1378 ± 188	4.47 ± 0.59 (112)	76.36 ± 5.05 (112)	102.3 ± 3.1 (112)	81	43.5 ± 3.3 (93)	

Table 5
Physical characteristics of bettongs that survived 18 months of exposure to cats (Cat Survivors) compared with new bettongs recruited during exposure to cats (Cat Recruits). Bettongs in the source population before translocation (Source Before) and at 22 months after translocation (Source After) are also shown. Significant differences between both recruits and survivors to the source population are highlighted in bold.

	n	Sex	Body condition index	Head length (mm)	Pes (mm)
Cat Survivors	117	All	4.67 ± 0.44	77.89 ± 5.86 (57)	103.9 ± 4.1
	68	M	4.64 ± 0.36	79.99 ± 5.74 (34)	**104.8 ± 3.5**
	49	F	4.70 ± 0.54	74.77 ± 4.56 (23)	102.7 ± 4.4
Cat Recruits	112	All	4.15 ± 0.60 (111)	73.38 ± 9.22 (94)	104.5 ± 3.6
	71	M	4.14 ± 0.54	74.47 ± 9.22 (56)	**105.3 ± 3.4**
	41	F	4.18 ± 0.71 (40)	71.76 ± 9.10 (38)	103.0 ± 3.5
Source Before	349	all	5.00 ± 0.81	Not recorded	103.2 ± 3.1
	204	M	5.10 ± 0.86		103.6 ± 3.0
	145	F	4.87 ± 0.74		102.5 ± 3.1
Source After	262	All	4.54 ± 0.61 (259)	76.35 ± 5.01 (259)	102.9 ± 3.5 (259)
	149	M	4.59 ± 0.63 (147)	76.34 ± 5.47 (147)	103.3 ± 3.7 (147)
	113	F	4.48 ± 0.59 (112)	76.36 ± 5.05 (112)	102.3 ± 3.1 (112)

large, male cats that had the highest probability of preying on bettongs (Marlow et al., 2015; Moseby et al., 2015a, 2015b), the presence of alternative prey such as rabbits and small mammals that are known prey items for cats (Dickman, 1996; Fitzgerald and Turner, 2000; Read and Bowen, 2001) may have reduced the predation rates on bettongs. Nevertheless, cats can be efficient predators of burrowing bettongs in the presence of rabbits and other alternative prey as evidenced by their contribution to the failure of numerous bettong reintroduction programs (Bannister et al., 2016; Christensen and Burrows, 1995; Moseby et al., 2011) and predation rates on related bettong species (Marlow et al., 2015; Priddel and Wheeler, 2004). As an example, 12% of 50 burrowing bettong carcasses found in a reintroduction at Heirisson Prong Sanctuary where rabbits were present were attributed to cat predation (Short and Turner, 2000).

In our study, the bettong population increased from 352 animals to 514 animals over 18 months (Moseby, unpublished data), further evidence that selection pressure was low. This may also have been a result of desexing the male cats before addition which may have influenced their hunting behaviour. Sexually intact male cats were found to be more aggressive than neutered males in free-roaming cats studied in Israel (Finkler et al., 2011).

An alternative explanation is that selection occurred but was undetected in our individual survival comparisons due to the small sample size of radio-collared animals, measurement of inappropriate traits and the large numbers of assumed mortalities. Although we trapped intensively over several sessions, the increase in population size suggests that many of the assumed mortalities may still have been alive but not re-trapped after release. This would have obscured any survival comparisons between individuals due to a high number of assumed unconfirmed mortalities. However, the method of using capture as evidence of individual survival has been used in previous studies (Armstrong and Perrott, 2000; Bertolero et al., 2007; Boon et al., 2008). Indeed individual capture history forms the basis of one of the most common methods of estimating survival in capture mark recapture studies (Otis et al., 1978). Determining unequivocal survival is a challenge for studies conducted at large spatial scales, such as this study, and highlights a need to radio-collar as many animals as possible to precisely determine the fate of individuals.

Population level changes provide some evidence that selection may have occurred after exposure to cats. Male bettongs exposed to cats had longer feet and females had smaller heads, whilst both sexes had lower body condition indexes at 18–22 months after release. However, when age effects were excluded, male pes was the only physical trait significantly different between mature and young adults in the cat-exposed treatment compared to controls. The smaller female head measurements and lower body condition index differences were found only within the adult animals recruited into the cat exposed population during the 18 months after release and could be due to age differences

rather than selection. However, subadults were excluded from the measurements and head measurements and body size are known to change rapidly in some mammal species in relation to their environment (Meiri et al., 2008). Non-lethal effects of predation can include changes to body mass and size (Creel and Christianson, 2008). For example, Banks et al. (1999) found rabbit body mass increased when predation risk was reduced. Additionally, island species can increase their body size rapidly simply due to isolation and/or reduced competition for resources (Millien, 2006). Unfortunately, the inability to divide the source population bettongs into cohorts for comparison with bettongs exposed to cat predation means we were unable to determine if head and body condition changes were due to selection or age-related phenotypic differences.

Our study was conducted over a short time frame but we nevertheless detected significant differences in one physical trait (male pes length) as a function of cat exposure. Since this change was consistent between both animals released into the cat treatment paddock and those recruited into the population after release it may represent phenotypic plasticity but is more likely to represent selection based on the consumptive effects of predation. Longer pes measurements in male bettongs exposed to cats could confer a survival advantage in term of improved escape speed or larger body size, making them less vulnerable to cat predation. Ecological invasions have been shown to trigger selection in resident native species and cause morphological changes due to the consumptive effects of predation, for example the hind legs of lizards exposed to invasive fire ants are longer in populations with longer exposure (Langkilde, 2009). Although longer pes measurements in the cat exposed bettong population may be a result of higher predation rates on smaller individuals, pes length was not a significant predictor of survival for bettongs released into the cat treatment paddock. This discrepancy may be caused by the large number of assumed rather than known mortalities used in the individual survival analysis or due to difficulties in detecting slight phenotypic changes in the low sample size of radiocollared individuals.

Although 18 months appears possibly too short to create detectable phenotypic evolution, there are examples where rapid selection has occurred under human-induced change or environmental pressure (Hendry et al., 2008; Phillips and Shine, 2005; Thompson, 1998). This rapid change is usually in species with short generation times and there are few if any examples of predators inducing phenotypic change in prey over less than one generation. Conversely, predators can change prey behaviour rapidly (Berger et al., 2001; Childress and Lung, 2003; Schmitz et al., 1997) and managers already recognize that genetic changes can occur over short time frames in animals subjected to captive housing as they adapt to captive conditions (Williams and Hoffman, 2009). Our understanding of the evolutionary timeframes necessary for prey species to maintain or acquire appropriate responses to introduced predators is poorly understood. We plan to continue

exposing bettongs to cat predation over longer time periods and measure intergenerational change.

It is possible that selection was occurring during our study on traits that we did not measure. Precisely identifying the traits that may confer a survival advantage is difficult because there is a potentially infinite number of traits that could be measured, some traits are difficult to measure and it is conceivable also that the traits which confer survival benefits may have relatively small and/or interactive effects. Whilst we measured traditional physical traits, such as sex, weight, condition, pes length and testes width, we did not measure other physical traits that could influence survival when living with predators, such as running speed, agility, reflexes, and endurance. Behavioural traits such as aggression, boldness, vigilance and flight initiation distance have been measured in bettongs previously (West et al., 2017) and some have been related to the trap docility scores measured in our study (West et al., unpublished data). However, behavioural traits recorded from trapped individuals are limited to those related to movement or aggression and may not be relevant to effective anti-predator behaviour.

Although our results are somewhat inconclusive, the changes in some physical traits in cat exposed bettongs suggests that *in situ* predator exposure has some effect but that weak selection may prevent detection of individual differences in survival. Apart from the physical changes we measured, there are other encouraging signs that *in situ* predator exposure may prove to be an effective way to facilitate long term co-existence between introduced predators and prey; bettongs were able to survive in the presence of feral cats; there is evidence of differential survival in previous reintroductions where some individual bettongs survived longer than others (Moseby et al., 2011); there are significant consistent differences in behaviour between individual bettongs that are related to anti-predator responses (West et al., unpublished data) and bettongs within the cat treatment have shown improved anti-predator responses over time suggesting they can learn to be more predator-aware (West et al., 2017). In other studies, previously naïve survivors have been shown to modify their behaviour after direct or vicarious experiences with predators (Berger et al., 2001). Finally, in some reintroductions, behaviour of individuals has been shown to be related to post-release survival (Bremner-Harrison et al., 2004).

Increasing the predation pressure in the cat treatment and monitoring survival of successive generations reintroduced into new areas where predators are present will allow *in situ* predator exposure and accelerated selection to be further tested as a tool to improve co-existence of exotic predators and native prey. Improving the responses of naïve prey to novel predators using evolutionary techniques is a bold and novel strategy that is firmly focused on the long term goal of co-existence between novel and introduced species. Following Carroll et al. (2014), we believe that a closer integration of evolutionary biology and reintroduction biology in future studies will enable us to test whether manipulating patterns of selection can improve conservation outcomes.

Acknowledgments

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