



# Exposure to a novel predator induces visual predator recognition by naïve prey

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## Abstract

The “life-dinner principle” posits that there is greater selection pressure on the species that have more to lose in an interaction. Thus, based on the asymmetry within predator-prey interactions, there is an advantage for prey to learn quickly, especially in response to novel, introduced predators. Here, we test the “learned recognition” hypothesis that posits that naïve prey species’ ability to recognise and respond to introduced predators can be induced through experience. We quantified the behavioural response of initially predator-naïve burrowing bettongs (*Bettongia lesueur*) that had been living in the presence (for 8–15 months) and absence of an introduced predator (feral cats—*Felis catus*) to models of cats, a herbivore (rabbit (*Oryctolagus cuniculus*)), novel object (plastic bucket) and no object (control). We expected that if bettongs recognised cats as a threat, they would be more wary in the presence of cat models than either rabbit models, buckets or the control. Bettongs living without predators did not modify their behaviour in response to the cat model, but spent more time cautiously approaching the rabbit model compared with the control. However, bettongs living with cats spent more time cautiously approaching the cat model compared with the rabbit, bucket and control. Our results are consistent with the learned recognition hypothesis which suggests that a predator-naïve prey species ability to recognise novel predators is inducible through experience. Our finding suggests that antipredator responses of reintroduced species could be improved prior to release by exposing them to predators under carefully controlled conditions.

## Significance statement

Predator-prey interactions have played a strong selective factor in the evolution of predator avoidance behaviour by prey. In order for prey to appropriately and successfully respond and avoid predation, it is essential that prey species recognise a predatory threat in the first place. The isolation of prey species on predator free islands, geographically isolated continents (such as Australia) and predator-free fenced reserves, means that prey are increasingly isolated from predator-driven natural selection processes. We studied the behavioural response of a population of initially predator-naïve burrowing bettongs that had been living in the presence (for 8–15 months) and absence of feral cats, (an introduced predator). Our results show that predator-naïve prey species’ ability to recognise novel predators is inducible through experience.

**Keywords** Antipredator behaviour · Burrowing bettong · Learned recognition hypothesis · Ontogenetic experience · Visual discrimination

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## Introduction

If prey fail to escape a predation event, they lose their life, whilst the predator simply loses their meal. The “life-dinner principle” posits that there is greater selection pressure on the species that have more to lose in an interaction (Dawkins and Krebs 1979). It is assumed that this asymmetry within the predator-prey system results in an unequal selection pressure in favour of the prey. Prey must evolve more rapidly than predators, thereby leaving predators less able to exploit them (Brodie and Brodie 1999).

There is a large body of literature on the invasion of novel predators and their effects on predator-naïve prey. Within ecosystems in which predators are newly introduced, their impacts are often most severe during the initial phase of invasion, compared with the chronic phase, where native prey may learn to respond to novel enemies (Bytheway et al. 2016). Some prey are able to innately recognise their predators (Veen et al. 2000; Apfelbach et al. 2005; Epp and Gabor 2008; Steindler et al. 2018), whilst others have the ability to learn how to respond to an introduced predator (Griffin et al. 2001; Epp and Gabor 2008; Anson and Dickman 2013; Bytheway and Banks 2019). The role of learned behaviour and naïveté in predator recognition are often unclear and confounded (Martin 2014) due to a lack of knowledge of evolutionary and ontogenetic history of prey species. Based on the natural asymmetry within the predator-prey system, there is an advantage for prey to learn quickly (Dawkins and Krebs 1979), especially in response to novel, introduced predators.

The degree to which antipredator behaviour towards a novel, introduced predator may be learnt or induced and the time frame over which this may occur is of considerable theoretical interest. The “prey naïveté” hypothesis suggests that animals isolated from predators over both ontogenetic and evolutionary time scales may lose antipredator behaviour that is costly and no longer relevant (van Damme and Castilla 1996; Blumstein and Daniel 2005). For example, a number of species isolated on islands appear to have responded to isolation from predators by reducing antipredator vigilance behaviour (Beauchamp 2004; Blumstein and Daniel 2005), as well as other behaviours, such as reduced wariness (Cooper et al. 2014). However, we do not expect that novel predators will remain eternally novel.

The “learned recognition” hypothesis suggests that through lifetime experience with predators, naïve prey may enhance their ability to recognise and respond to predators (Turner et al. 2006). This ability to develop learnt antipredator recognition skills towards previously evolutionary and ontogenetically unfamiliar predators has been shown in fish (Ferrari et al. 2005; Ferrari 2014; Holmes and McCormick 2010), birds (Maloney and McLean 1995) and mammals (Mineka and Cook 1988; Griffin et al. 2000; Webb et al. 2008).

An understanding of the time frames over which predator recognition behaviour may be learnt or induced is also of great practical conservation interest. The more rapidly a naïve prey can learn to recognise predators, the better their chances of survival (McCormick and Holmes 2006). The introduction of novel predators has led to the rapid loss of “naïve” endemic species within a number of areas (Engbring and Fritts 1988; Johnson 2006). Since the introduction of predators such as the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) (Woinarski et al. 2015), Australia has experienced the highest contemporary mammal extinction rate in the world, with 18 species driven extinct over the last two centuries (Johnson 2006). Prey naïveté towards introduced predators has resulted in limited reintroduction and translocation success (Moseby et al. 2011, 2012). Reintroduction of naïve species that have already failed to survive in the presence of novel predators will ultimately result in failure, unless the reintroduced animals acquire survival skills not present in the original populations (McLean et al. 1996; Moseby et al. 2016).

Antipredator behaviour may diminish over ontogenetic (Carrete and Tella 2015) or evolutionary time (Blumstein and Daniel 2005), but the question still then remains: how long does it take to acquire antipredator behaviour for species that have had minimal evolutionary and no previous ontogenetic exposure to predators? Previous studies have shown that species are able to adapt readily to change, with species learning to recognise threats from introduced and novel species within several generations (Berger et al. 2001; Phillips and Shine 2006; Webb et al. 2008). If a species has the ability to learn to respond to a novel threat, than they should be flexible in their responses to predation (Brown and Chivers 2005; Berger et al. 2010). Individuals should be at a selective advantage if they are capable of reliably assessing local predation risk and adjusting the intensity of their antipredator behaviour to match their current risk (Chivers et al. 2001; Brown and Chivers 2005; Ferrari et al. 2005; Ferrari 2014). The challenge, however, is to determine what level of environmental change or predation pressure will encourage learning and, ultimately, adaptation rather than extinction (Phillips and Shine 2006).

Much of the literature investigating the evolved abilities of wild prey to recognise cues associated with novel predator species cannot control for variation in ontogenetic exposure to predators (Carthey and Banks 2012, 2014, 2016; Anson and Dickman 2013; Bytheway and Banks 2019). Conducting experiments that manipulate the populations of reintroduced threatened species and introduced predators is rarely possible due to the large spatial extent required for manipulations, and legal, political and ethical considerations. Here, we test the idea that a prey species’ ability to visually recognise novel predators can be induced as a result of ontogenetic experience. We did this by quantifying the behavioural response of wild burrowing bettongs (*Bettongia lesueur*)

living within fenced enclosures at Arid Recovery Reserve, South Australia, in the presence (for 8–15 months) and absence of feral cats, to taxidermy models of cats (an introduced novel predator) and European rabbits (*Oryctolagus cuniculus*—a herbivore), plastic buckets (a novel object) and no object (control).

Although we could not control for individual ontogenetic experience, the introduction of a known number of feral cats into a managed, fenced population of reintroduced burrowing bettongs provided a rare opportunity to test a naïve prey species' ability to recognise and respond to introduced predators, at a population level, as a result of experience.

Previous research has not explored the role that visual recognition has played in the response of burrowing bettongs to predators. If a lack of experience with predators influenced the ability of bettongs living in the “no predator” enclosure to recognise models, we would expect that bettongs should show a similar response to models of cats (a potential predatory threat), as they would to rabbits (a herbivore) and our novel object (a bucket of similar height as our cat model). We would expect that bettongs should show a greater, generalised response to all the models than to the control (no object).

If predator visual recognition abilities are inducible through experience, we expected that bettongs coexisting with cats, in the “cat enclosure”, should have greater responses to the predator model than rabbits, with which they have had some ontogenetic exposure to within the enclosure and to our novel object (plastic bucket) and the control (no object).

## Methods

### Study species

Burrowing bettongs (Fig. 1) are a small (800–2000 g), nocturnal, omnivorous, burrowing macropod (Short and Turner 1993),

which live in large social groups of 20–40 individuals (Sander et al. 1997). It is the only species of macropod to construct and live in warrens and burrows (Short and Turner 1993).

Burrowing bettongs were driven extinct on mainland Australia in the twentieth century due primarily to predation by introduced red foxes and feral cats (Short and Turner 1993, 2000), as well as competition with rabbits and pastoral activities (Short and Turner 2000). Prior to their extinction on the mainland, burrowing bettongs' natural predators would have included dingoes (*Canis lupus dingo*) (Allen and Fleming 2012) and wedge-tailed eagles (*Aquila audax*). Populations of burrowing bettongs persisted on Bernier, Dorre and Barrow Islands off the coast of Western Australia (Short and Turner 1993, 1999, 2000). Burrowing bettongs within this study were sourced from populations that have experienced low levels of cat predation within their recent evolutionary history (see Supplementary Material for further details). Since their introduction to Arid Recovery in 1999/2000, burrowing bettongs have been completely isolated from all mammalian predators (Richards et al. 2008; Moseby et al. 2011).

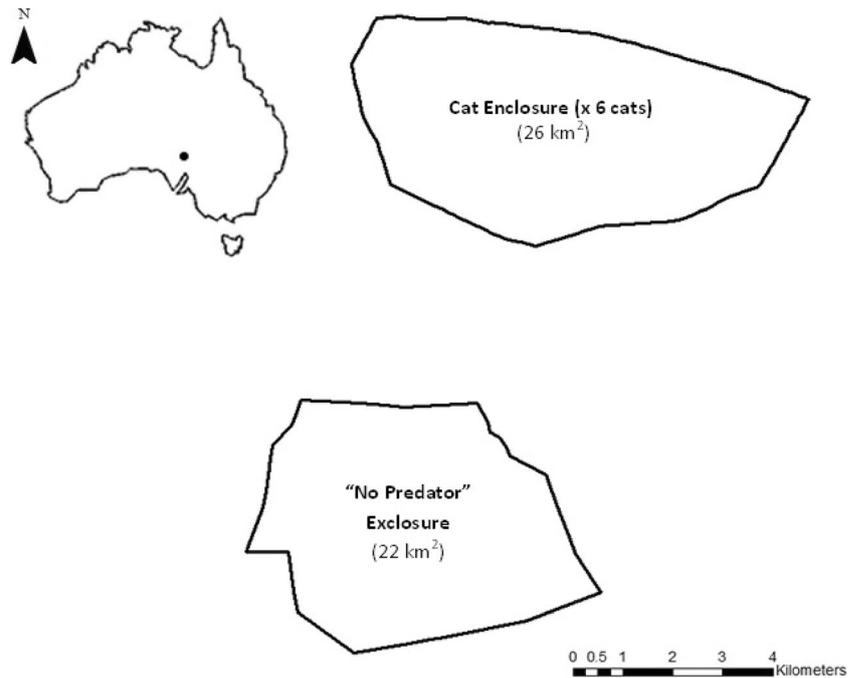
### Study site

The study was conducted within two fenced areas within the Arid Recovery Reserve, South Australia (12,300 ha, 30°29' S, 136°53' E). All mammalian predators, including cats and foxes are absent and excluded from the 22 km<sup>2</sup> “no predator” section of the reserve (Fig. 2). Between October and December 2014, a total of 352 burrowing bettongs were reintroduced into the 26 km<sup>2</sup> “cat enclosure” (Fig. 2). When the release of bettongs into the cat enclosure commenced in 2014, there was one cat of unknown sex present. Five additional feral cats were added between 6 and 8 months after the initial bettong release in 2014; however, three were only detected during the study period. Rabbits were absent from the

**Fig. 1** Burrowing bettong (*Bettongia lesueur*)



**Fig. 2** Map of Arid Recovery Reserve showing areas of where the model presentation studies were conducted. The “no predator” enclosure was free of placental predators, with bettongs reintroduced between 1999 and 2000. Within the “cat enclosure”, one cat of unknown sex was present in 2014, with five additional cats added between 6 and 8 months after the initial release of bettongs in 2014



“no predator” enclosure and at low densities in the “predator enclosure” (West et al. 2017).

### Population level vigilance behaviour field methods

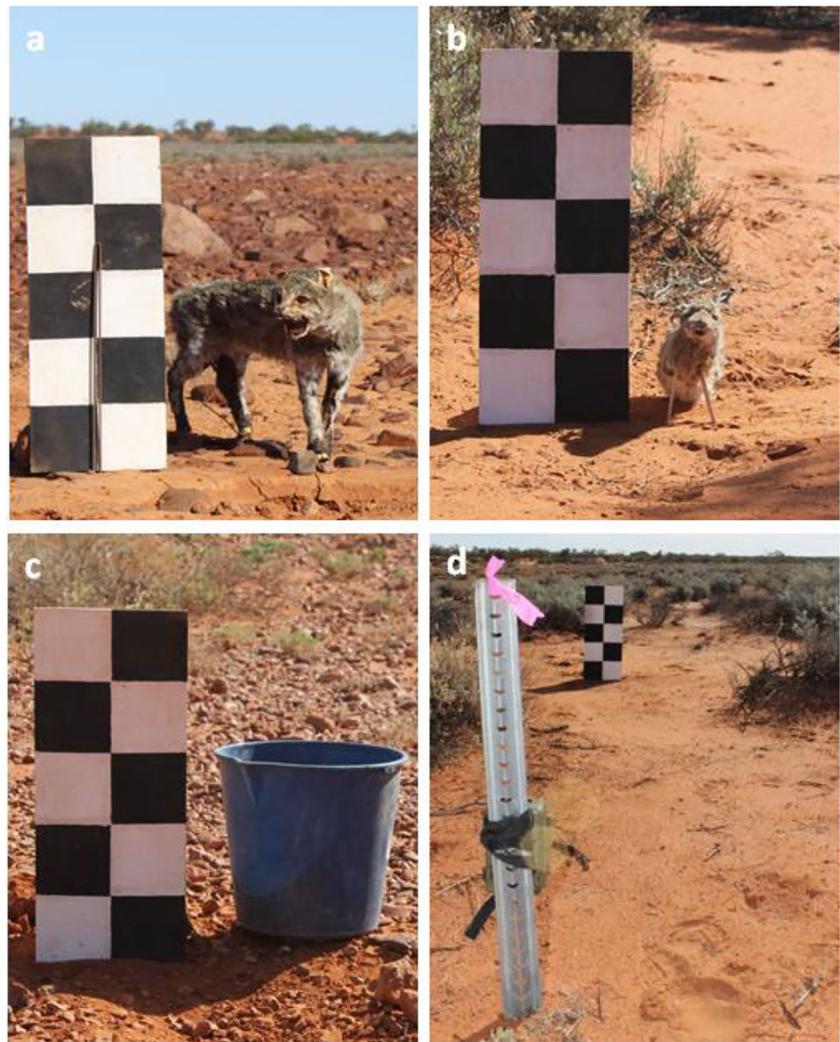
We utilised a video footage from infrared motion sensor cameras placed at foraging trays to gauge the behavioural responses of bettongs living within fenced enclosures in the presence and absence of feral cats, to taxidermy models of cats, rabbits, novel object (bucket) and control (no object). Because burrowing bettongs are nocturnal, it is difficult to perform focal observation experiments. We conducted experiments in the “no predator” and “cat enclosure” simultaneously.

A total of 96 feeding stations, with 48 in the “no predator” enclosure and 48 in the “cat enclosure”, were established along roads with sites set approximately 400 m apart. Experiments were conducted over 16 nights (8 nights in October 2015 and 8 nights in March 2016). Experiments were conducted across two time periods in an attempt to increase sample size, with sampling period accounted for statistically as a repeated measure. Burrowing bettongs were allowed to acclimate to forage at the feeding stations for one night. After one night of acclimatisation, treatments (cat, rabbit, bucket or control) were randomly allocated to all stations for the second night, regardless if bettongs were positively identified foraging at the stations on night 1. Treatments were applied only once per site per year (Table 1). We used six life-size taxidermy models of cats (Fig. 3a) and rabbits (Fig. 3b), and 9.3-L

**Table 1** The number of (a) foraging stations ( $n$ ) by treatment type deployed during the 2015 and 2016 sampling periods, (b) number of stations that received at least one visit and (c) the total number of stations from which videos were analysed for bettong behavioural responses

| Enclosure     | Year  | Treatment |    |    |     |    |    |         |    |    |        |    |    |       |    |    |
|---------------|-------|-----------|----|----|-----|----|----|---------|----|----|--------|----|----|-------|----|----|
|               |       | Bucket    |    |    | Cat |    |    | Control |    |    | Rabbit |    |    | Total |    |    |
|               |       | a         | b  | c  | a   | b  | c  | a       | b  | c  | a      | b  | c  | a     | b  | c  |
| No predator   | 2015  | 12        | 11 | 9  | 12  | 10 | 7  | 12      | 7  | 5  | 12     | 11 | 8  | 48    | 39 | 29 |
|               | 2016  | 12        | 12 | 7  | 12  | 12 | 6  | 12      | 12 | 9  | 12     | 11 | 10 | 48    | 47 | 32 |
|               | Total | 24        | 23 | 16 | 24  | 22 | 13 | 24      | 19 | 14 | 24     | 22 | 18 | 96    | 86 | 61 |
| Cat enclosure | 2015  | 12        | 8  | 5  | 12  | 7  | 7  | 12      | 9  | 7  | 12     | 6  | 4  | 48    | 30 | 23 |
|               | 2016  | 12        | 9  | 6  | 12  | 6  | 5  | 12      | 4  | 6  | 12     | 8  | 4  | 48    | 27 | 21 |
|               | Total | 24        | 17 | 11 | 24  | 13 | 12 | 24      | 13 | 13 | 24     | 14 | 8  | 96    | 57 | 44 |

**Fig. 3** Three dimensional models used to represent **a** cat, **b** rabbit, **c** novel object (plastic bucket) and **d** camera set up at the control, which had no physical model present. Cats are an introduced “novel” predator, rabbits are a non-threatening herbivore and buckets are a non-threatening novel object. A scale is provided in the pictures, with each square measuring 100 cm<sup>2</sup>



plastic buckets (Fig. 3c), to quantify the response to a novel object and a control (no objects, Fig. 3d) that allowed us to measure spontaneous behavioural change in the absence of a stimulus presentation.

To investigate whether sample sites were independent of one another, we tested for spatial autocorrelation in the residuals of the fitted values for each behaviour, in each enclosure, using Moran’s index ( $i$ ), calculated in the spatial analyst module of ArcGis v10.3 (Table S1 in the Supplementary information). Spatial autocorrelation occurs when the value of a variable at any one location in space can be predicted by the values of nearby locations. If spatial autocorrelation exists, then sampling units are not independent of one another. Despite burrowing bettongs travelling an average of 500–600 m per night (Short and Turner 2000) and although it is possible that burrowing bettongs visited multiple stations, analysis showed experimental sites were independent (Table S1) and treatments were randomised across sites.

Each station comprised a metal post, positioned approximately 2 m from the road, supporting a Bushnell

Trophy Cam (Bushnell, USA), Scoutguard SG550V or Scoutguard Zeroglow (Scoutguard, Australia), infrared motion sensor video camera. Cameras were mounted 50–150 mm off the ground and were programmed to take 60-s videos when triggered, to enable species identification and observe behavioural responses to the model types. There was a 10-s interval between possible triggers, from dusk until dawn (1700–0700 h). A food lure, approximately 100 g dog pellets (Home brand Adult Dog Food Beef & Vegetable; Woolworths, Australia) was buried beneath the surface and mixed into the inedible substrate from the surrounding environment, approximately 5 m from the road. We swept a 10-cm circle directly surrounding the food lure to detect tracks and validate visitation. The site was checked the following day for signs of foraging. Sites were reset with approximately 100 g of dog pellets in the late afternoon for the second night (treatment night) and were accompanied with a pre-determined randomised visual treatment.

## Behavioural scoring

We employed an “expert-based” (EB) method to reduce the number of variables for analysis and create five main behavioural groups, based upon the initial observations of experimental videos, relying on ethological knowledge and video observations (Table 2) (Mazzamuto et al. 2018). With the EB approach, the researcher defines groups of behaviours, with each group related to specific behavioural responses. We then scored video recordings  $\leq 60$  s using the event recorder JWatcher (Blumstein and Daniel 2007) from which we calculated the proportion of time allocated to each behaviour. As behavioural scoring only commenced when a bettong was within the field of view of the camera, we were unable to analyse total length of time for each behaviour. Since prey may habituate to the presence of a cue when not accompanied by a predator (Parsons and Blumstein 2010), we quantified the behaviour of the first burrowing bettong to approach and/or forage at the site. Videos with more than one individual foraging were excluded to reduce the influence of conspecific presence on the behavioural response to the treatments. We were unable to group individuals into age demographics due to the limitations of infrared camera technology.

Data was recorded blind in regard to enclosure; however, it was not possible to record data blind in terms of treatment because our study involved quantifying the behaviour of animals interacting with a visual stimulus. Behavioural scoring was conducted by the same person, with behavioural assessments standardised before behavioural scores were recorded.

## Analysis of behavioural data

Because feral cats were present only in one section of the reserve and absent throughout the remainder of the reserve, our treatments were by necessity spatially segregated such

that, according to a strictly statistical approach, our experimental design does not allow us to run a model comparing “no predator” vs. “cat enclosure” (Hurlbert 1984). However, we have compared and contrasted their responses to the treatments within each location, in order to assess the influence of lifetime experience on bettong predator visual recognition abilities and behaviour towards cats.

We used a generalised estimating equation (GEE) model with independent error structure and binomial distribution in SPSS-22 (IBM Corp. Armonk, NY, USA) to investigate if bettong visitation to feeding stations on treatment night was dependent on the type of model placed at the feeding station. The response variable was visit (1) or no visit (0).

To test whether model type caused burrowing bettongs to allocate different proportions of time to composite behaviours, in the absence and presence of cats, we fitted a series of generalised estimating equation (GEE) models with an independent error structure and linear distribution. The factor in our model was model type (cat, rabbit, bucket and control). As we could not distinguish between individual burrowing bettongs and account for the possibility of non-independence between observations, we included foraging station location as a repeated measure in our models. Due to an unbalanced design as a result of low sample sizes across sampling periods (October 2015, March 2016), sampling period was made a covariate in the models. For the analysis of “investigate model” behaviours, in which an individual investigated models through smell and/or touch, the control was removed from the analysis, because no model was present. In instances where the effect of model type was significant ( $P < 0.05$ ), we used Bonferroni-adjusted significant tests for post hoc analysis to examine planned pairwise comparisons for differences in response to each model type (cat vs. rabbit, cat vs. bucket, cat vs. control, rabbit vs. bucket, rabbit vs. control and bucket vs. control), as we wished to understand the pattern of responses.

**Table 2** Ethogram of burrowing bettong (*Bettongia lesueur*) behaviour

| Behaviour category | Behaviour         | Description  |
|--------------------|-------------------|--|
| Wary approach      | Bi-pedal sniff    | Looks and/or sniffs air whilst standing upright on hind limbs                  |
|                    | Prone sniff       | Looks and/or sniffs the air and/or ground whilst standing on all four limbs    |
|                    | Slow approach     | Moves slowly towards feeding station   |
| Fast approach      | Fast approach     | Moves quickly and directly towards feeding station                             |
| Foraging           | Vigilant foraging | Chews with its head up and observing surroundings                              |
|                    | Relaxed foraging  | Forages for food and chews with its head down without observing surroundings   |
| Investigate model  | Investigate model | Investigates model type through smell and/or touch                             |
|                    | Chew model        | Attempts to eat the model type   |
| Retreat            | Recoil            | Suddenly spring or flinch back away from the feeding station and/or model type |
|                    | Retreat           | Retreats away from feeding station and/or model type                           |
| Out of sight       | Out of sight      | Out of sight of camera   |

## Results

### Visits to station

There was no effect of model type (Wald  $\chi^2 = 0.304$ ,  $P = 0.859$ ) in the “no predator” and “cat enclosure” (Wald  $\chi^2 = 0.272$ ,  $P = 0.873$ ) on visitation to feeding stations (Table 1). Thus, bettongs were equally likely to visit the stations regardless of the specific model present.

### Behavioural response to model type

#### No predator treatment

In the “no predator” enclosure, there was a significant effect of model type on the proportion of time that burrowing bettongs allocated to wary approach (Wald  $\chi^2 = 9.636$ ,  $P = 0.022$ , Table 3, Fig. 4(a)) and retreat (Wald  $\chi^2 = 8.380$ ,  $P = 0.039$ , Table 3, Fig. 4(c)) behaviours. We found no significant effect of model types in the “no predator” enclosure on the proportion of time burrowing bettongs allocated to foraging, fast approach and investigate model behaviours (Table 3, Fig. 4(b)–(e)). There was no spatial autocorrelation in the residuals of the fitted values for any of the analysed behaviours in the “no predator” enclosure (Table S1 in the Supplementary information). These results indicate that the feeding stations were independent for the purpose of our analysis. Within the no predator area, planned post hoc comparisons revealed that burrowing bettongs spent significantly more time in wary approach behaviour when approaching the rabbit compared with the control (Bonferroni, rabbit vs. control,  $P = 0.043$ ; Fig. 4(a)). Bettongs did not modify time spent warily approaching the cat or bucket compared with the control (Bonferroni, cat vs. control,  $P = 0.074$ ; bucket vs. control,  $P = 0.909$ ; Fig. 4(a)). There was no significant difference between the proportion of time spent in wary approach behaviours between the three model types (Bonferroni, bucket vs. cat,  $P = 0.999$ ; bucket vs. rabbit,  $P = 0.614$ ; and cat vs. rabbit,  $P = 0.999$ ; Fig. 4(a)). There were no significant differences

**Table 3** Results from generalized estimating equations model testing for differences between model types (cat, rabbit, bucket and control—no visual) on the mean proportion of time spent on each behaviour by burrowing bettongs (*Bettongia lesueur*) in the “no predator” enclosure

| Enclosure type | Behaviour     | df | Wald $\chi^2$ | $p$     |
|----------------|---------------|----|---------------|---------|
| No predator    | Wary approach | 3  | 9.636         | 0.022** |
|                | Forage        | 3  | 7.661         | 0.054   |
|                | Retreat       | 3  | 8.380         | 0.039** |
|                | Fast approach | 3  | 1.215         | 0.749   |
|                | Investigate   | 2  | 1.604         | 0.448   |

Values with a double asterisk indicate significant differences

in the proportion of time spent by bettongs retreating between the models (Bonferroni, cat vs. rabbit,  $P = 0.999$ ; cat vs. bucket,  $P = 0.999$ ; and rabbit vs. bucket,  $P = 0.252$ ) and control (no object) (Bonferroni, cat vs. control,  $P = 0.999$ ; rabbit vs. control,  $P = 0.458$ ; and bucket vs. control,  $P = 0.999$ ). A detailed list of planned comparisons conducted for behaviours recorded in the no cat treatment may be found in Table S2 in the supplementary information.

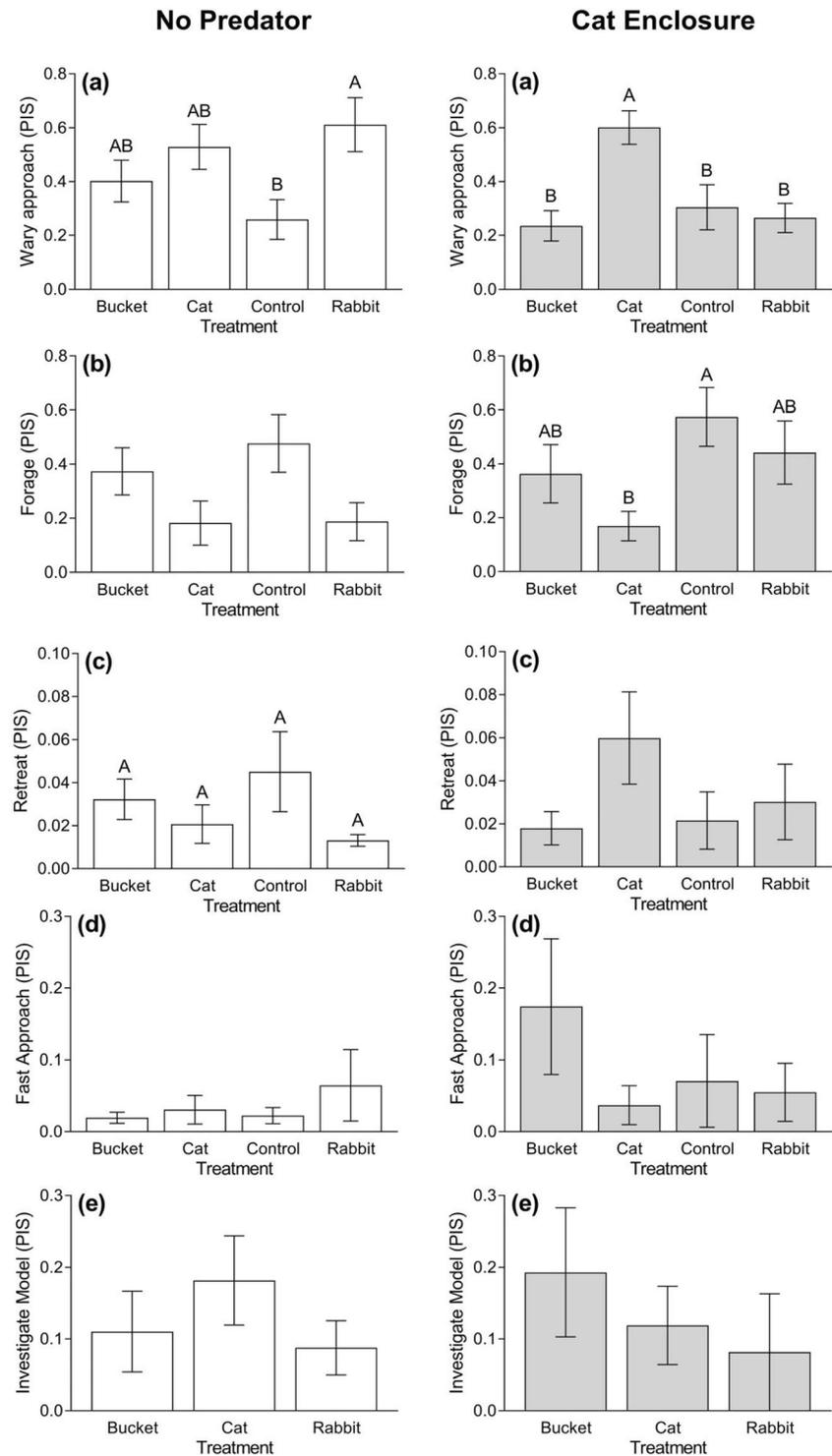
#### Cat enclosure treatment

In the “cat enclosure”, there was a significant effect of model type on the proportion of time that burrowing bettongs allocated to wary approach (Wald  $\chi^2 = 36.052$ ,  $P \leq 0.005$ , Table 4, Fig. 4(a)) and forage (Wald  $\chi^2 = 15.864$ ,  $P \leq 0.005$ , Table 4, Fig. 4(b)) behaviours. We found no significant effect of model type in the “cat enclosure” on the proportion of time burrowing bettongs allocated to retreat, fast approach and investigate model behaviours (Table 4, Fig. 4(c)–(e)). There was no spatial autocorrelation in the residuals of the fitted values for any of the analysed behaviours in the “cat enclosure” (Table S1 in the Supplementary information). These results indicate that the feeding stations were independent for the purpose of our analysis. Post hoc tests revealed that within the “cat enclosure”, burrowing bettongs spent significantly more time in wary approach behaviour when investigating the cat model than they did the rabbit (Bonferroni, cat vs. rabbit,  $P \leq 0.005$ ; Fig. 4(a)), the bucket (Bonferroni, cat vs. bucket,  $P \leq 0.005$ ; Fig. 4(a)) and the control (no model) (Bonferroni, cat vs. control,  $P = 0.02$ ; Fig. 4(a)). There were no differences in the proportion of time allocated to wary approach between the rabbit, novel object and control (Bonferroni, rabbit vs. bucket,  $P = 0.999$ ; rabbit vs. control,  $P = 0.999$ ; and bucket vs. control,  $P = 0.999$ ; Fig. 4(a)). Where cats were present, planned comparisons revealed that bettongs spent significantly less time foraging at the cat models than the control (Bonferroni, cat vs. control,  $P \leq 0.005$ ; Fig. 4(b)). There was no significant difference in time allocated to foraging between the models (Bonferroni, cat vs. rabbit,  $P = 0.208$ ; cat vs. bucket,  $P = 0.647$ ; and rabbit vs. bucket,  $P = 0.999$ ; Fig. 4(b)), nor between the rabbit and novel object compared with the control (Bonferroni, rabbit vs. control,  $P = 0.999$  and bucket vs. control,  $P = 0.727$ ; Fig. 4(b)). A detailed list of planned comparisons conducted for behaviours recorded in the “cat enclosure” may be found in Table S3 in the supplementary information.

## Discussion

The results from our experiments are consistent with the learned recognition hypothesis and our a priori predictions that a prey species’ ability to visually recognise predators is inducible through experience. Bettongs living

**Fig. 4** The mean ( $\pm 1$  SEMs) proportion of time in sight (PIS) that burrowing bettongs allocated to the behaviours in response to model types in the “no predator” and “cat enclosure” study areas, (a) wary approach, (b) foraging, (c) retreat, (d) fast approach and (e) investigate model. Only behaviours that had significant differences between model types have letter above the bars (e.g. A or B) Different letters identify pairwise comparisons that are statistically different ( $P < 0.05$ )



without predators did not modify their behaviour in response to the cat model, but spent more time cautiously approaching the rabbit model compared with the control. In stark contrast, bettongs living with cats adjusted their behaviour to the presence of cat models.

Although there was variation in visitation rates between the study areas, with feeding stations visited 89.6% of the time in the

“no predator” area, compared with 59.4% in the “cat enclosure”, this is likely to be a result of bettong population density rather than a response to treatments. The population density of bettongs in the “no predator” area was nearly three times greater than that of the “cat enclosure” (Moseby et al. 2018) during the study period. As we did not run a model comparing the study areas, variation in visitation rates does not have a bearing on the results

**Table 4** Results from generalised estimating equations model testing for differences between model types (cat, rabbit, bucket and control—no visual) on the mean proportion of time spent on each behaviour by burrowing bettongs (*Bettongia lesueur*) in the “cat enclosure”

| Enclosure type | Behaviour     | df | Wald $\chi^2$ | <i>p</i>          |
|----------------|---------------|----|---------------|-------------------|
| Cat enclosure  | Wary approach | 3  | 36.052        | $\leq 0.005^{**}$ |
|                | Forage        | 3  | 15.864        | $\leq 0.005^{**}$ |
|                | Retreat       | 3  | 4.023         | 0.259             |
|                | Fast approach | 3  | 2.321         | 0.508             |
|                | Investigate   | 2  | 0.999         | 0.607             |

Values with a double asterisk indicate significant differences

discussed. Further to this, although bettongs were equally likely to visit stations across the two experimental sites, regardless of the specific model present, bettongs did adjust their behavioural responses accordingly.

Burrowing bettongs in the predator-free enclosure appeared to respond to the rabbit model compared with the control (no model), expressed through wary approach behaviour. Bettongs did not differentiate their wary approach behaviour between the models (cat, rabbit and bucket). One hypothesis to explain this response is that rabbits may be competitors with burrowing bettongs and this competition has resulted in the evolution of an aversive response to rabbits. The similarities in response of burrowing bettongs to a potential competitor (rabbits), a predator (cat) and control (bucket) could also reflect the limited discriminative ability of this species, based on their lack of ontogenetic experience with predators, rather than the fact that it is not a fearful response.

Bettongs in the cat enclosure allocated the most time to wary approach behaviour when a cat model was present, compared with the rabbit, bucket and control (no object). That bettongs in the cat enclosure differentiated their response to the visual models and were more wary towards the cat models suggests that visual recognition is associated with a specific predatory threat and is consistent with previous studies that have investigated learned behavioural response towards predators (Maloney and McLean 1995). In a study of New Zealand robins, predator-naïve robins exposed to predatory treatments developed strong predatory responses (Maloney and McLean 1995). In addition, our results support the ideas proposed by Berger et al. (2001) and Griffin et al. (2001) who suggested that if prey are exposed to a novel threat and survive the encounter, then their response towards predators may persist.

Although analysis found that there was a significant effect of model type in the proportion of time burrowing bettongs in the predator-free enclosure allocated to retreat behaviour, post hoc analysis suggested that there was no significant differences in the proportion of time spent by bettongs retreating in response to model type (bucket, cat, rabbit and control—no visual). This non-result may be a caveat of the type of post hoc analysis used.

Bonferroni post hoc analysis adjusts significance levels to control for type I error rates in multiple testing situations (Quinn and Keough 2002). Although Bonferroni post hoc analysis provides great control over type I error, it is very conservative when there are lots of comparisons, causing comparisons to have decreasing power as the number of comparisons increases (Quinn and Keough 2002).

Previous studies have found that animals living with predators commonly trade off foraging with antipredator vigilance (Bednekoff and Lima 1998; Griffin et al. 2000; Beauchamp 2015). Bettongs in the no predator enclosure did not adjust their foraging behaviour in response to the different model treatments. Our results suggest bettongs living with no predators were “predator naïve” because they did not significantly alter their behavioural responses between the model types, such as a predator, herbivore (rabbit), novel object (bucket) and the control (no object). We presume that this naïveté was due to their lack of ontogenetic and minimal evolutionary experience with cats (Atkins et al. 2016).

In contrast to the bettongs living in the predator-free environment, bettongs that were coexisting with cats spent the least proportion of time foraging when cat models were present. As the quality of food (dog kibble) was standardised across both study areas, “no predator” and “cat enclosure”, variation in bettong foraging behaviour appears to be indicative of bettongs trading off the risk of predation versus the reward of high-quality food (McArthur et al. 2014). Previous studies have also similarly found that experience, rather than evolutionary history, strongly influences prey response to predators (Berger et al. 2001; Martin 2014). For example, studies of learning in fish have found that fish learned to respond more intensely to predator cues associated with high risk (Ferrari et al. 2005). This implies that while a species may not respond appropriately upon first encountering a predator (Mirza et al. 2006), experience and rapid learning may play a key role in the development of antipredator behaviours.

Visual predator recognition sometimes depends on cues such as shape or the presence of frontally located eyes (Curio 1993; Coss and Goldthwaite 1995). Carnivores have binocular vision, whilst herbivores have eyes on the sides of their heads (Blumstein et al. 2000). Previous studies have also suggested that prey may use the apparent size of models to assess risk (Evans et al. 1993; Blumstein et al. 2002). If the stimulus size was important, we would expect similar responses to both the cat and bucket models because they are of similar height (Fig. 3a, c). Bettongs living in the no predator enclosure did not appear to alter their behaviour according to model size or eye location, with no significant differences in behaviour towards cat, bucket and rabbit models. It is possible that olfactory cues associated with the taxidermy mounts explained some variation in the burrowing bettong response. However, taxidermy mounts were treated in the same tub of tanning solution, for the same duration of time (30 days) and were moved across both study sites at random. If there was a significant effect of olfactory cues

associated with the mounts, we would have expected to see this response across both the “no predator” and “cat enclosure” study areas and this was not the case.

Further to this, studies have also found that the eyesight of nocturnal species is more acute and variable than previously recognised (Bearder et al. 2006). Although nocturnal mammals are primarily orientated by olfactory and audible senses (Mascalzoni and Regolin 2011), it has been found that nocturnal mammals are well adapted to low light environments (Heesy and Hall 2010; Mascalzoni and Regolin 2011), allowing them to visually discriminate objects (Wynne and McLean 1999). A study of pupillary mobility in four species of marsupial with differing lifestyles, including burrowing bettongs, found that bettong’s retinas are extremely light sensitive, which assists in the detection of shapes and movement, which is crucial for predator detection (Arrese 2002).

It is possible that the use of taxidermy models may underestimate the predatory response bettongs may display if exposed to a live predator. This has been noted in a study of peahens, which emitted louder antipredator calls when exposed to a live predator, compared with a model (Yorzinski and Platt 2012). It was assumed that this response reflected the greater threat a live predator posed compared with a model in the captive experiments. It is also possible that bettongs may have responded differently if multiple cues, such as visual and olfactory, had been presented simultaneously. According to the sensory complement hypothesis, multiple cues which suggest a predation risk combine in an additive manner, evoking an increased antipredator response (Lima and Steury 2005). This was the case in a study of multi-modal risk assessment in wild eastern grey squirrels (*Sciurus carolinensis*), which had a greater response to audio/visual signals of alarm compared with either audio or visual signals alone (Partan et al. 2009). Since our experiment aimed to determine whether bettongs could learn to visually recognise predators in the first instance, we did not add a second modality. Future studies assessing bettong predator recognition may have to combine modalities in an additive manner to determine whether behavioural responses stay the same, are reduced or become enhanced.

Prior to this study, bettongs at Arid Recovery had no ontogenetic experience and minimal evolutionary exposure to placental predators. Although the founding population of bettongs at Arid Recovery may have had a brief evolutionary exposure to cats on Bernier Island (Atkins et al. 2016) and Herrison Prong (Short and Turner 2000), the results from the “no predator” enclosure suggest that this minimal evolutionary experience did not influence their visual recognition abilities.

Prior to the extinction of bettongs on the mainland, bettongs would have been naturally predated upon by dingoes (Allen and Fleming 2012). Although dingoes and cats are both members of the same order, Carnivora, these predators differentiate in their preference of food sources and hunting styles

(Bradshaw 2006). Dingoes utilise a conservative feeding strategy (Corbett and Newsome 1987), preferring large, infrequent meals. In contrast, cats are exclusively solitary hunters, and as such hunt prey that are typically smaller in body mass than themselves, resulting in cats having to eat several small meals per day (Bradshaw 2006). Thus, and despite some morphological similarities, these predators may differ in some key behavioural traits, which render the defences of Australian native prey species ineffective against these introduced predators (Cox and Lima 2006).

The ability of bettongs living within the “cat enclosure” to visually discriminate a predator from an herbivore and novel object suggests that ontogenetic experience is essential to develop and induce learned predator recognition. These findings are consistent with previous studies that have reported learnt predator recognition (Brown et al. 2006; Ferrari et al. 2006, 2010) and the strong role that learning (Martin 2014) and level of predation risk (Chivers and Smith 1994; Bøving and Post 1997; Griffin et al. 2001; Bytheway and Banks 2019) play in structuring antipredator responses.

A caveat of this study is that we were unable to test for the mechanisms leading to our results. As burrowing bettongs are a social species, it is possible that individuals may have exploited the expertise and individually acquired predator avoidance behaviours of others, through social learning (Kavaliers et al. 2001; Griffin and Evans 2003); however, due to the limitations of this study, we were unable to test for this. As we were studying a wild population of bettongs, we were unable to determine whether a bettong had encountered a predation event with a cat and survived. As such, we can only make assumptions that bettongs living within the “cat enclosure” have encountered cats, either directly or indirectly (through social learning), within their lifetime, in comparison with bettongs living within the “no predator” enclosure, who have no ontogenetic experience with cats. We further make the assumptions that through individual experience or through social learning, it may be presumed that learned recognition occurs because there is an evolutionary advantage for prey to learn quickly in response to novel predators.

From a conservation perspective, understanding the rate of behavioural adaptation by prey to a novel predator is of great importance. Given the likelihood of exposure of burrowing bettongs to the threat of predation by cats (whether individually and/or socially), this study provides a unique insight into the influence that predation pressure can have in the development of antipredator behaviours and the time frames over which this can occur. We know that bettongs have had minimal evolutionary exposure to novel predators, such as cats. We know that the bettongs at Arid Recovery have had no ontogenetic exposure to placental mammalian predators within the “no predator” enclosure, and we also know how long bettongs have been exposed to cat predation within the “cat enclosure”. This is in stark contrast to other studies in which

history of predator exposure is unknown (Banks et al. 2002; Anson and Dickman 2013).

Our results suggest that bettongs with no ontogenetic and minimal evolutionary exposure to feral cats can rapidly (within 8–15 months of predator exposure) acquire predator recognition abilities after exposure to a novel predator. From a reintroduction perspective, this suggests that predator-naïve prey may be able to develop antipredator responses induced through experience. Such learned antipredator responses could be utilised in pre-release prey training through exposure of prey individuals to predators under carefully controlled conditions (Moseby et al. 2016). However, we acknowledge that demonstrating the utility of predator exposure as a pre-release strategy requires actually demonstrating that in situ predator exposure confers a fitness advantage.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the South Australian Wildlife Ethics Committee, conducted under animal ethics APEC Approval Number 1/2014 *Tackling Prey Naivety in Australia's Threatened Mammals*, and ACEC Approval Number 15/19A, in accordance with The Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (1997).

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