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ORIGINAL ARTICLE

Deep evolutionary experience explains mammalian responses to predators

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Abstract
Prey may have ontogenetic experience, evolutionary experience, or both types of experiences with their predators and how such experiences influences their ability to identify their predators is of great theoretical and applied interest. We capitalized on predator-free exclosures containing populations of native burrowing bettongs (*Bettongia lesueur*) and introduced rabbits (*Oryctolagus cuniculus*) that ensured we had knowledge of our subjects' ontogenetic experiences with predators and asked whether evolutionary experience influenced their visual predator discrimination abilities. Rabbits evolved with red foxes (*Vulpes vulpes*) and wolves (*Canis lupus*) but had less than 200 years of prior exposure to dingoes. The rabbit population we studied had been exposed to dingoes (*Canis dingo*) and foxes 8 months prior to our study and had heightened responses to red fox models, but not dingo/dog (*Canis dingo*/*Canis familiaris*) models. The insular burrowing bettong population had no ontogenetic exposure to mammalian predators, brief evolutionary exposure to domestic dogs and possibly dingoes, and a deeper evolutionary history of exposure to thylacines (*Thylacinus cynocephalus*)—another large mammalian predator with convergent body morphology to dingoes/dogs but no evolutionary or ontogenetic exposure to foxes. Bettongs showed a modest response to the dingo/dog model and no response to the fox model. These results are consistent with the hypothesis that deep evolutionary history plays an essential role in predator discrimination and provides support for the multipredator hypothesis that predicts the presence of any predators can maintain antipredator behavior for other absent predators.

Significance statement
Prey may have ontogenetic experience and or evolutionary experience with their predators. How such experiences influence prey species' ability to identify their predators is of significance to theory on the evolution of antipredator response and to improve the success of translocations and reintroductions for conservation purposes which often fail because of predation on predator naïve prey. Here, we show that prey recognition for two prey species with limited or no ontogenetic exposure to predators, rabbits, and burrowing bettongs was greatest toward the predator to which they had the longest period of coevolution. The results are consistent with the hypothesis that evolutionary history plays an essential role in predator discrimination and provides support for the multipredator hypothesis that predicts the presence of any predators can maintain antipredator behavior for other absent predators.

Keywords Antipredator behavior · Visual predator discrimination · Multipredator hypothesis

Introduction

Prey may have ontogenetic experience, evolutionary experience, or both types of experiences with their predators. How such experiences influence prey species ability to identify

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predators is of considerable theoretical and applied interest (Cox and Lima 2006; Carthey and Banks 2012). Theoretically, we need to better understand the conditions that lead to the maintenance or loss of predator discrimination abilities and antipredator behavior under relaxed selection that occurs when a historically important predator is no longer present (Lahti et al. 2009). This loss can happen through extinctions of historically important predators, range shifts, and isolation on islands (e.g., Blumstein 2002).

From a practical perspective, we need to understand how predator naïveté works to better understand the consequences of predator introductions and reintroductions as well as to understand how to improve the success of translocations and reintroductions for conservation which often fail because of predation on predator-naïve prey (Moseby et al. 2015). Indeed, predation by introduced predators, especially mammalian predators, is a major factor responsible for the extinction of wild vertebrate populations and the failure to successfully reintroduce endangered vertebrates in many parts of the world (King 1984; Savidge 1987; Biggins et al. 1999; Johnson 2006; Moseby et al. 2011).

The Australian mammal fauna has had a long exposure to mammalian predators including thylacines (*Thylacinus cynocephalus*), Tasmanian devils (*Sarcophilus harrissii*) quolls (genus *Dasyurus*), and more recently (from about 3000 yBP), dingoes (*Canis dingo*) (Letnic et al. 2012a, b). However, native mammals, especially ground-dwelling mammals in the arid zone within a critical weight range (35–5500 g) have experienced massive population reductions or extinction in the last 200 years following the introduction of novel mammalian predators: feral cats (*Felis catus*) and red foxes (*Vulpes vulpes*) (Burbidge and McKenzie 1989; Johnson and Isaac 2009).

Endangerment of Australian mammals has been attributed in part to prey naïveté, the failure of an animal to mount an effective antipredator defense. Prey naïveté has multiple levels, which are dependent on the level of experience with a predator (Banks and Dickman 2007). The highest level of naïveté is firstly a failure to recognize a predator. Secondly, a naïve animal may recognize a predator but respond incorrectly to evade attack. Finally, a naïve animal may respond correctly but still fail to evade capture. Strong selection imposed by predators may quickly drive prey population through the levels of prey naïveté and thus enhance prey species abilities to recognize and evade predators (Anson and Dickman 2013).

Antipredator responses exist on a continuum between "hardwired" responses that are effective on first contact with a predator and entirely learned behaviors that require experience (Kats and Dill 1998; Berger et al. 2001). The longevity and strength of evolutionary experience with a specific predator may influence the degree to which the response is hardwired (Griffin et al. 2000; Tortosa et al. 2015). Thus, ontogenetically naïve animals may still display antipredator behaviors when exposed to cues associated with the presence of a coevolved predator for the first time (Blumstein 2006). However, because it is difficult to control for the lifetime experience of predators in populations of wild prey, isolating the evolved response can be problematic.

We capitalized on populations of endangered burrowing bettongs (*Bettongia lesueur*) and introduced European rabbits (*Oryctolagus cuniculus*) living within predator-free exclosures with known ontogenetic experiences with predators to ask the question if evolutionary experience with predators (for the bettongs, limited experience of dogs/dingoes and no exposure to red foxes; for the rabbits, a long period of coevolution with red foxes and more recently, dingoes) predict visual predator discrimination abilities. To answer this question, we filmed the behavior of bettongs and rabbits at experimental feeding stations at which we had placed models (Fig. 1) of dingoes/dogs, red foxes, kangaroos (a harmless herbivore to which both species have ontogenetic exposure) and a procedural control.

Methods

Study site

We studied bettongs and rabbits within the Arid Recovery reserve, a 123-km^2 complex of predator-free exclosures in central South Australia (Moseby et al. 2009) in the Austral spring of 2014 (30° 22′ S, 136° 54′ E). At the time of our study, the reserve comprised six paddocks. Four of these paddocks contained a total population of more than 2000

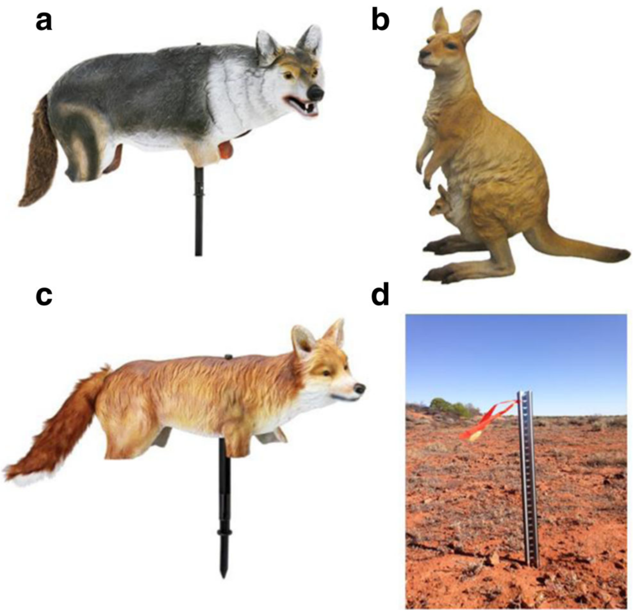

Fig. 1 Three-dimensional models used to represent **a** dingoes/dogs, **b** kangaroos, **c** foxes, and **d** the control. Dingoes/dogs and foxes are predators and the kangaroo is a non-threatening species with which bettongs and rabbits have coexisted at Arid Recovery. Note pictures are not to scale

burrowing bettongs but no rabbits or mammalian predators. Two of the paddocks contained rabbits but no burrowing bettongs. Dingoes and foxes were eliminated from the paddocks containing rabbits in early 2014, and cat populations were present in these two paddocks at low numbers at the time of the experiment.

Study species

Burrowing bettongs

Burrowing bettongs are small, nocturnal marsupials (body mass 800–2000 g) unique among Macropodoidea as the only species to construct and live in burrows (Short and Turner 1993). Prior to European settlement, bettongs were widespread across the Australian continent, but natural populations are now limited to three islands off the coast of Western Australia (Short and Turner 2000). The bettongs introduced to Arid Recovery in 1999–2001 were captured from wild populations on Bernier Island and Heirisson Prong (a translocated population from Dorre Islands in Western Australia, Finlayson and Moseby 2004).

These island populations of bettongs have had limited contact with mammalian predators because the islands were isolated from the mainland about 8000 years ago due to rising sea levels (Short et al. 1997). Prior to isolation, these animals would have been exposed to marsupial predators, thylacines, and western quolls (*Dasyurus geoffroyii*; Letnic et al. 2012a, b). However, at the beginning of the twentieth century, the bettongs were known to have been exposed to domestic dogs (*Canis familiaris*) for at least 10 years when the source islands were used as a hospital and also when livestock grazing was conducted on the islands (Shortridge 1910; Stringmore 2010). During this time, dogs were brought to the island as working dogs for livestock production and as companions and pets for the Aboriginal people who hunted bettongs (Shortridge 1910; Stringmore 2010). Thus, it is likely that the islands' bettongs were hunted by dogs accompanied and unaccompanied by people as is typically the case around human settlements where dogs are not restrained (Vanak and Gompper 2009). It is also possible that Aboriginal people accompanied by dingoes visited the islands from time to time during the Holocene, as other similarly isolated islands off the Western Australian coast have documented archeological evidence of human habitation (Dortch and Morse 1984), but no surveys of prehistoric archeology have been undertaken on Bernier and Dorre Islands (Stringmore 2010). Non-mammalian predators also depredate bettongs on the source islands and at Arid Recovery, including eagles (*Aquila audax*, *Haliaeetus leucogaster*) and monitor lizards (*Varanus* spp.) (Short and Turner 1999).

European rabbits

European rabbits were introduced to Australia in the nineteenth century. Rabbits are primarily nocturnal, although sometimes active during the day (Lombardi et al. 2003). Rabbits invaded arid South Australia in the late nineteenth century and now occupy most of the former range of burrowing bettongs (Robley et al. 2001). Rabbits evolved with red foxes within their native range as well as wolves—a dingo congener. The rabbit population we studied at Arid Recovery was contained within exclosures that were free of red foxes and dingoes at the time of the study but had contained foxes and dingoes as recently as 8 months earlier. Rabbits are the primary prey of both foxes and dingoes in the region of arid Australia where the study was conducted (Cupples et al. 2011). Because juvenile rabbits in our study area emerge from warrens in August and September and populations in the austral spring (September–November) are dominated by young of the year (Bowen and Read 1998), we assume that most of the rabbits at Arid Recovery at the time of our study (August–November) had not been exposed to dingoes or foxes. However, rabbits that were more than 8 months old at the time of the study may have had ontogenetic exposure to both dingoes and foxes. Nonetheless, despite variation in the ontogenetic exposure of rabbits at Arid Recovery to predators, rabbits have had a long period of evolutionary exposure to red foxes in Europe and Australia and a shorter (<150 years) period of coevolution with dingoes since their introduction to Australia. Other predators known to prey upon rabbits present in the exclosures of Arid Recovery are feral cats, eagles, and varanid lizards.

Methods

Experimental rationale

To determine if evolutionary experience with predators can predict prey species visual predator discrimination abilities, we filmed prey species behavior at experimental feeding stations at which we placed models of dingoes/dogs, red foxes, kangaroos, and a procedural control. If the duration of coevolution with predators influenced their ability to recognize predators, we would expect that rabbits should have a larger antipredator response to red foxes than to dingoes/dogs, and that the Arid Recovery burrowing bettongs should show greater responses to dingoes/dogs than red foxes. If burrowing bettongs or rabbits recognized dingoes/dogs or foxes as a threat, we expected that they should have greater responses to the predator models than kangaroos, a harmless herbivore with which they have had ontogenetic exposure to at Arid Recovery and to our procedural control, which was a metal post of similar height

(4 cm wide) as our dingo/dog and kangaroo models. It was not possible to record data blind because our study involved focal animals in the field.

Data collection

We established feeding stations >100 m apart on sand dunes, prime habitat for both species, to control for variation in the surroundings, which can influence an animal's perceived predation risk (Lima and Dill 1990; Schultz et al. 2004). Burrowing bettongs readily dig through the sand to obtain food, so for assays of bettong behavior, 100 g of oats was evenly distributed through a 20-L bucket of sand that was buried flush with the ground surface. Rabbits do not dig when foraging, so for assays of rabbit behavior, oats were placed on the surface of the sand, although for methodological consistency, the sand underneath the oats was disturbed using a shovel.

At each feeding station, we deployed motion-sensor night vision cameras (Scoutguard KGV680V and Bushnell 8MP Trophy Cam HD). Each feeding station was accompanied by one predator or control model, placed ~4 m from the food reward. The choice of model deployed at each feeding station was determined by a random number generator. Our models (Fig. 1) included the following: dingo/dog (life-size Lucky Duck™ rubber hunting decoys, body size 94 cm × 20.3 cm × 40.6 cm, affixed to a post, with faux fur tails and glass eyes), red foxes (life-size Lucky Duck™ rubber hunting decoys, body size 35.6 × 22.8 × 15.2 cm, affixed to a post, with faux fur tails and glass eyes), a non-threatening kangaroo (a stationary 51-cm tall hard resin garden statue by Garden Statues and Ornaments, Australia: http://www.gardenstatuesandornaments.com.au/), and a control treatment that consisted of pink flagging on a metal post that, like the tails of the dingo/dog and fox models, could move in the wind. To avoid habituation to the feeding stations and models, each feeding station was deployed for one night only. In total, we deployed a total of 161 feeding stations for rabbits and 147 for bettongs across 13 nights (3 in August 2014, and 10 in October/November 2014). In many cases, and for a variety of reasons (human errors positioning or programming the cameras, battery failure, models being knocked over, and birds consuming the food before our target species had an opportunity to forage), the cameras only operated for part of the night or failed completely and we were thus unable to obtain or utilize the video footage.

Data analysis

We used generalized linear mixed models with a binomial distribution to investigate if bettong and rabbit visitation to feeding stations was dependent on the type of model placed at the feeding stations. The response variable was visit (1) or no visit (0). Because the experiments were conducted in multiple paddocks and on multiple nights, paddock and night were specified as random effects in the models.

To analyze bettongs' and rabbits' time budgets in response to models placed at feeding stations, we focused on quantifying the first minute of video footage of the first visit of a bettong or rabbit to a feeding station. We did so because this eliminated any variation in the potential food reward present (which could influence responsiveness) and the influence of previous visitation to foraging stations by conspecifics. We developed an ethogram that focused on locomotion, foraging, and vigilance and was suitable for both species (Table 1). We then scored behavioral transitions using an event recorder (Cowlog version 2.0; Hänninen and Pastell 2009). After scoring, we calculated the proportion of time in sight allocated to each behavior and then combined these into four categories. "Low vigilance" was comprised of feeding, locomotion, intraspecies interactions, and exploratory behaviors. "Wary approach" was a slow and cautious movement toward the feed tray. "Looking" comprised all activities where the animal paused to acquire more information by moving its head about their surroundings while not actively ingesting food. "Escape" was scored when an animal fled the feeding tray. We also quantified the duration of time that animals were "Out of Sight," scored when an animal was out of view of the camera.

We fitted linear mixed effects models (LME) in SPSS v22 to test whether bettongs and rabbits allocated different amounts of time measured as the duration or proportion of time in sight to these composite behaviors as a function of treatment. Because the response variables were not normally distributed, we rank-transformed each variable prior to analysis (Quinn and Keough 2002). Because the experiments were conducted in multiple paddocks and on multiple nights, paddock and night were specified as random effects in the models. By design, we fitted LMEs for each variable and in instances where the treatment effect was significant ($P < 0.05$), we calculated planned comparisons for the difference in response to each pair of stimuli using Fisher least significant difference tests because each comparison was meaningful (Quinn and Keough 2002). Thus, for all variables, we investigated the planned contrasts dingo/dog vs. fox, dingo vs. kangaroo, dingo/dog vs. control, fox vs. kangaroo, fox vs. control, and kangaroo vs. control.

Results

Visits to stations

There was no effect of the models on visitation to feeding stations (Table 2) by bettongs ($F = 0.856$, $df = 3, 111$, $P = 0.466$) or rabbits ($F = 0.332$, $df = 3, 158$, $P = 0.802$). Thus, both bettongs and rabbits were equally likely to visit the stations regardless of the specific treatment present.

Table 1 Ethogram used to classify behaviors of bettongs and rabbits

Behavior Category	Behavior	Description	Vigilance category
Locomotion	Fast approach	Animal moves quickly and directly towards feed tray	Low vigilance
	Slow approach	Animal moves slowly towards feed tray	Wary approach
	Fast retreat	Animal retreats quickly from feed tray	Escape
	Slow retreat	Animal retreats slowly from feed tray	Low vigilance
	Vigilant lateral movement	Other movement (neither towards or away from feed tray) while remaining observant	Looking
	Relaxed lateral movement	Other movement (neither towards or away from feed tray) while not observing	Low vigilance
Foraging	Vigilant feeding	Animal chews with its head up and observing surroundings	Looking
	Relaxed feeding	Animal eats with its head down without observing surroundings. Also includes attempts to eat the feed tray.	Low vigilance
Vigilance	Looking	Sniffing or looking	Looking
Interaction with environment	Vigilant interaction with model	Animal interacts with model (predator, non-threat or control) while remaining vigilant	Looking
	Relaxed interaction with model	Animal interacts with model (predator, non-threat or control) without remaining vigilant	Low vigilance
	Interacting with conspecifics	Interacting with conspecifics, including fighting and courtship	Low vigilance
	Interacting with other species	Interacting with other species	Low vigilance
Out of sight	Out of sight	Out of camera range	Hide

The ethogram summarizes behaviors by type and classifies them into categories used to analyze responses to stimulus presentation

Behavioral response to stimuli

Burrowing bettongs: Bettongs displayed a tendency to modify the time they allocated to looking as a function of treatment ($F = 2.557$, $df = 3$, 95.666, $P = 0.060$, Fig. 2a). The plot of looking versus treatment (Fig. 2a) suggests that they spent more time looking at feeding stations with dingo/dog models than other models. Similarly, there was a weak, non-significant, effect of treatment on bettongs' allocation of time to escape behavior ($F = 2.231$, $df = 3$, 95.792, $P = 0.090$; Fig. 2b). However, again, the plot of escape behavior versus treatment (Fig. 2b) suggests a trend toward bettongs allocating more time to escape behavior in the presence of the dingo/dog model. The experimental treatment had no effect on the amount of time that bettongs allocated to wary approach ($F = 1.924$, $df = 3{,}98.08$ $P = 0.131$; Fig. 2c), low vigilance ($F = 2.046$, $df = 3{,}96.190$, $P = 0.113$), or the time they spent out of sight ($F = 1.817$, $df = 3$, 96.326, $P = 0.158$).

Table 2 The number foraging stations visited by bettongs and rabbits by treatment

	Control	Dingo/dog	Fox	Kangaroo
Rabbit	22 (40)	24 (39)	25 (39)	25 (44)
Bettong	29 (33)	27 (28)	23 (26)	27 (28)

The number in parentheses indicates the total number of foraging trays deployed in each treatment for the bettong and rabbit experiments for which cameras functioned the entire night

European rabbits: Rabbits did not modify the time they allocated to looking as a function of treatment ($F = 0.116$, $df = 3{,}85.351$, $P = 0.951$, Fig. 3a). There was a significant effect of treatment on the proportion of time that rabbits allocated to escaping ($F = 7.522$, $df = 3$, 84.313, $P < 0.001$, Fig. 3b). Planned comparisons (Fig. 3b) revealed that rabbits spent more time in escape behavior with model foxes than they did at feeding stations with dingo/dog (Fishers LSD fox vs. dingo/dog, $P = 0.001$) and kangaroo models (fox vs. kangaroo Fishers LSD $P = 0.001$) or the control (Fishers LSD, fox vs. control, $P < 0.001$). Treatment also explained significant variation in the time rabbits were engaged in wary approaches ($F = 3.094$, $df = 3$, 85.717, $P = 0.031$, Fig. 3c). Planned comparisons (Fig. 3c) revealed that rabbits spent more time in wary approach at feedings stations with model foxes than they did at feeding stations with kangaroo models (fox vs. kangaroo Fishers LSD $P = 0.025$) and the control (fox vs. control Fishers LSD $P = 0.006$). There was no effect of treatment for the time that rabbits spent in low vigilance ($F = 0.679$, $df = 3$, 80.295, $P = 0.568$, Fig. 3d). Finally, there was an effect of treatment on the amount of time that rabbits spent out of sight ($F = 3.197$, $df = 3$, 82.367, $P = 0.028$, Fig. 3e). Planned comparisons (Fig. 3e) revealed that rabbits spent more time out of sight at feeding stations with fox models than with kangaroo models (fox vs. kangaroo Fishers LSD $P = 0.020$) or the controls (fox vs. control Fishers LSD, $P = 0.005$).

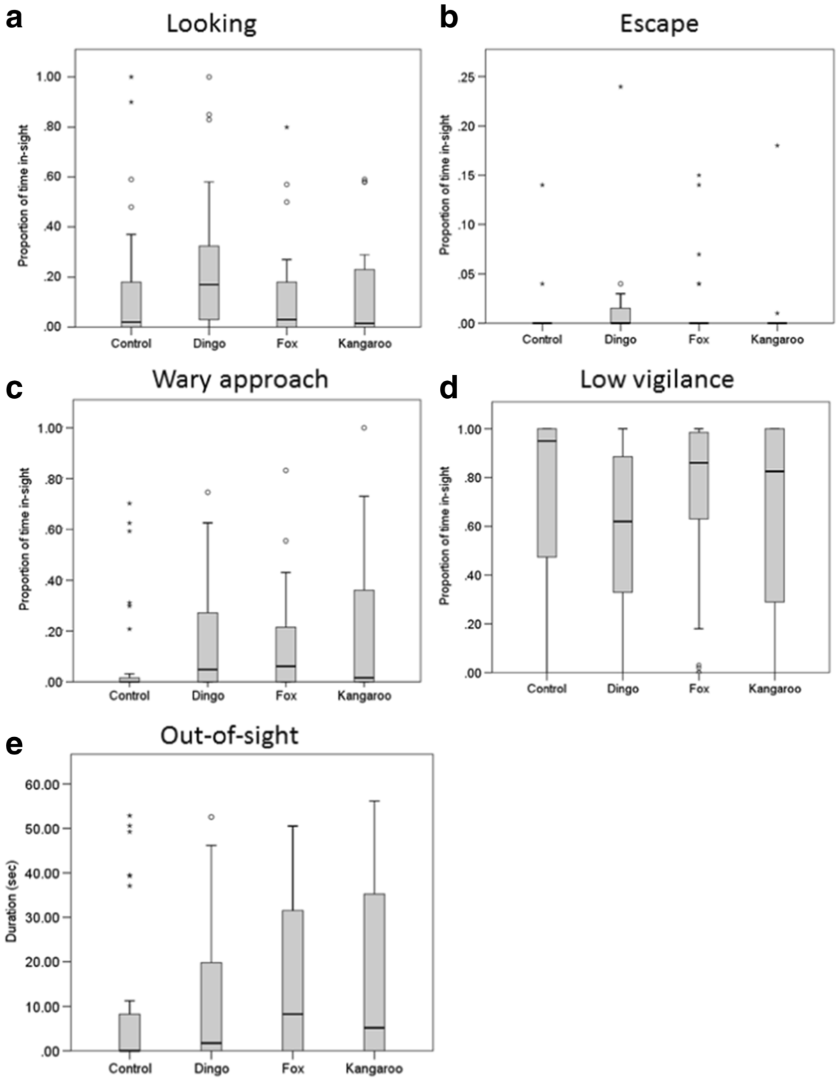

Fig. 2 Boxplots of the responses of burrowing bettongs to the deployment of predatory and control stimuli (dingoes/dogs $n = 28$, foxes $n = 23$, kangaroos $n = 26$, and a procedural control $n = 28$) in the first minute of visitation to foraging stations. The *box* indicates one quartile either side of the median, and the *bars* indicate 1.5 times the interquartile range. *Dots* and *stars* indicate outliers that fall outside the range of the *boxes* and *bars*. *Stars* indicate extreme outliers that have values more than three times the height of *boxes*. The median is indicated by the *lines within the boxes*

Discussion

The results of this experiment are consistent with the evolutionary exposure hypothesis of prey naïveté. While both burrowing bettongs and rabbits foraged on the supplementary food provided at our treatments, both species, while visiting the feeding stations, adjusted their antipredator behavior in the presence of a predator with whom they shared a longer evolutionary history but did not significantly adjust their behavior when in the presence of a predator they have had a comparatively short period of coexistence with. However, it is important to note that bettongs' responses to the dingo/dog models were weak in comparison to the rabbits' responses to foxes.

The homogeneity between treatments in our visitation results indicates that neither bettongs nor rabbits responded to the visual cues we presented by avoiding the area entirely. Avoidance behaviors are predicted to have the greatest influence on the outcome of a potential predator interaction; however, due to the greater opportunity cost (as compared to vigilance responses), they may be lost more readily under relaxed selection (Barrio et al. 2010). Alternatively, previous studies on rabbits have attributed a lack of avoidance response to scale-sensitive antipredator behavior, where behaviors may change at a larger scale than that studied (Barrio et al. 2010).

Instead of avoiding our sites entirely, rabbits and bettongs adjusted their antipredator behavior when in the presence of a predator with which they had greater evolutionary experience. These findings accord with our a priori predictions and suggest that rabbits and, to a lesser extent, bettongs were able to distinguish the predator species with which they had the longer period of coevolution from the other models and were not simply responding to the presence of the models regardless of the species they represented or the difference in size between the models.

Rabbits responded strongly to the fox models and tended to spend more time in wary approach, escaping, and out of sight at foraging stations where fox models were deployed. Indeed, rabbits did not adjust the amount of time looking, but rather

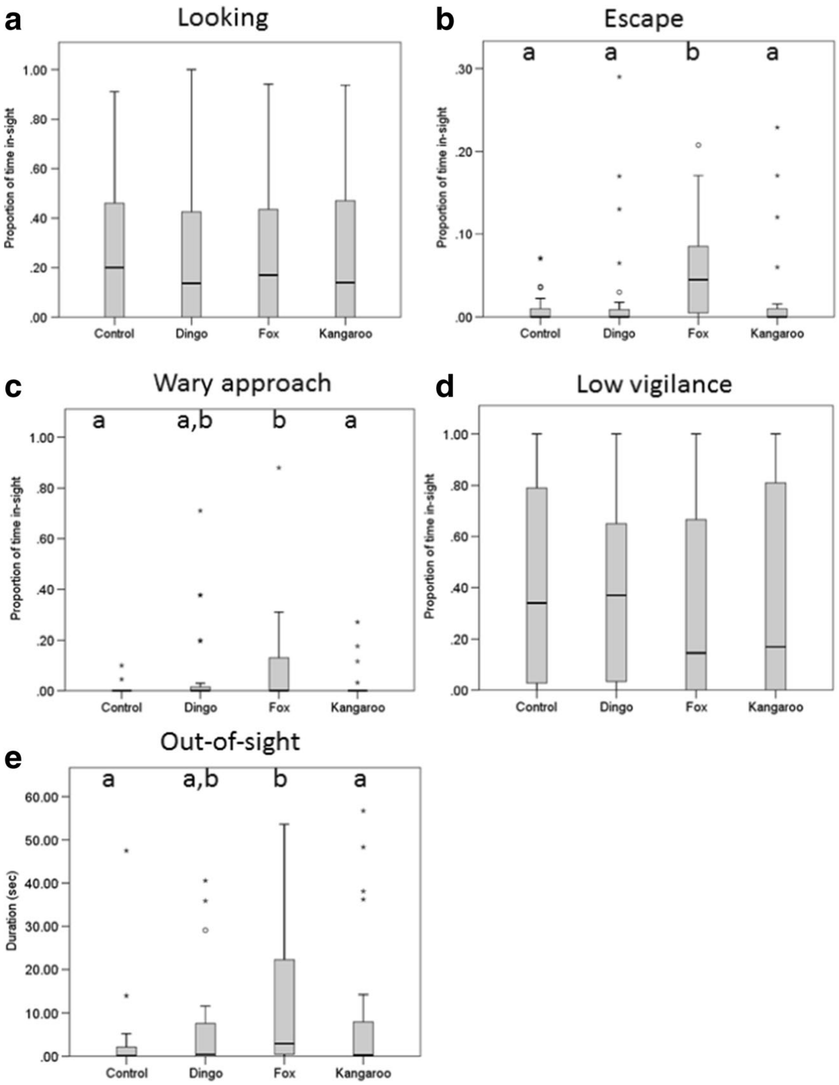

Fig. 3 Boxplots of the responses of rabbits to the deployment of predatory and control stimuli (dingoes/dogs $n = 23$, foxes $n = 24$, kangaroos $n = 25$, and a procedural control $n = 22$) in the first minute of visitation to foraging stations. The *box* indicates one quartile either side of the median, and the *bars* indicate 1.5 times the interquartile range. *Dots* and *stars* indicate outliers that fall outside the range of the *boxes* and *bars*. *Stars* indicate extreme outliers that have values more than three times the height of *boxes*. The median is indicated by the *lines within the boxes*. Similar letters (e.g., a or b) above the bars identify pairwise differences that were statistically indistinguishable ($P > 0.05$)

were more wary when approaching the feeding station, retreated quickly far more often, and spent more time away from the bait station where the fox model was present at the bait station. Remarkably, rabbits seemingly failed to respond to our dingo/dog models despite their evolutionary history with closely related wolves and given that the rabbits we studied had more than 100 years of evolutionary experience with dingoes in Australia. Moreover, this finding is perhaps even more remarkable because any rabbits older than 8 months at the time of the study are likely to have had ontogenetic exposure to dingoes at Arid Recovery.

In comparison to rabbits, bettongs displayed a muted response to the predator models. The weak responses may result from their limited ontogenetic and evolutionary exposure to mammalian predators on the source islands and more recently in the predator-free exclosures at Arid Recovery. However, bettongs tended to spend more time looking and escaping at foraging stations where dingo/dog models were deployed (Fig. 2a, b). This result suggests that despite complete ontogenetic naïveté, the bettongs at Arid Recovery may have some ability to discriminate the dingoes/dog models from the other models.

A plausible explanation for the apparent response of bettongs to the dingo/dog models could be that bettongs maintained an evolutionary response to the large-bodied thylacine which has remarkably convergent morphology with dingoes (Letnic et al. 2012a). On mainland Australia, thylacines were approximately dingo/dog-sized and thus would have similar silhouettes to our dingo/dog models (Letnic et al. 2012a). Alternatively, bettongs simply responded to the size of the models deployed at the stations and thus exhibited more wary behavior at the stations with the largest models—which were the dingo/dog models. Support for this explanation is provided by our observation that bettongs spent more time out of sight at the stations with the second largest model, the kangaroo, than they did at our controls. However, it is important to note that another study conducted at Arid Recovery found that bettongs had an ability to respond to the scent of dingoes, but not foxes (MH unpubl. data). Taken together, these results suggest that bettongs have a modest ability to identify dingoes/dogs but no ability to identify foxes. That bettongs can discriminate dingoes/dogs from other models is consistent with the idea that the Arid Recovery bettong population has undergone selection by thylacines, dingoes, or domestic dogs in the past.

Cox and Lima's (2006) archetype hypothesis would predict that a species with similar morphological adaptations to capture prey would elicit a similar antipredator response, especially with respect to visual cues which are remarkably convergent (Blumstein et al. 2000). Indeed, other studies suggest that archetypes can explain the ability of tammar wallabies (*Macropus eugenii*) to respond to evolutionarily and ontogenetically novel foxes (Blumstein et al. 2000). The archetype hypothesis could explain bettongs' responses to the dingo/dog models despite their brief period of evolutionary coexistence because they coevolved with the morphologically convergent and similarly sized thylacine prior to the isolation of the islands about 8000 yBP. However, neither bettongs nor rabbits responded in the same way to both the fox and dingo/dog models. This finding suggests perhaps that rabbits and bettongs perceive the differently sized fox and dingo as distinct archetypes, despite being members of the same family (Canidae). If so, this is notable because Family is often used as a proxy for archetype in predator recognition research (Cox and Lima 2006).

Escape behaviors are an important part of evading capture by predators (Blumstein 2006; Cooper and Blumstein 2015) but come with a cost of missed foraging and mating opportunities. Optimal foraging theory predicts that animals will only seek the reward if the risk is low enough (Brown 1988), and in insular populations, costly escape behaviors may be lost relatively quickly (Blumstein and Daniel 2005). Consistent with this idea, the Arid Recovery bettongs displayed a weak escape response to the dingo models.

Our finding that bettongs had some ability to discriminate dingoes/dogs from other stimuli even though they have been completely isolated from mammalian predators at Arid Recovery and are thought to have only some limited exposure to mammalian predators on the islands from which the populations were sourced are in broad support of the multipredator hypothesis (Blumstein 2006). The multipredator hypothesis predicts that species will retain antipredator behavior after isolation from them as long as they experience some risk of predation (Blumstein 2006; Blumstein et al. 2009). The retention of some antipredator behavior may be because at both Arid Recovery and the source islands, the bettongs were subject to predation by eagles and varanid lizards.

Our findings that bettongs' and rabbits' predator discrimination abilities are scaled with their period of evolutionary coexistence is consistent with previous studies examining the abilities of mammals to discriminate the scents and images of predators with which they have had varying periods of coevolution (Blumstein et al. 2000; Carthey and Banks 2012; Tortosa et al. 2015). Our results have implications for future reintroduction programs of burrowing bettongs and other mammals endangered by introduced predators because they suggest that naïveté toward introduced predators could be reduced if mammals were exposed to predators to create or select for abilities to recognize introduced predators (Moseby et al. 2015). However, it is important to add the caveat that the short time of coexistence between the island bettongs and dogs/dingoes together with only a weak capacity to recognize dingoes/dogs suggests that the ontogenetically naïve bettong population at Arid Recovery may not at the present time possess the appropriate suite of antipredator responses required to withstand predation by dingoes or other mammalian predators.

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Compliance with ethical standards All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors. Work was conducted under animal ethics APEC Approval Number 15/19A and in accordance with *The Australian Code of Practice for the Care and Use of Animals for Scientific Purposes* (*1997*).

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Conflict of interest The authors declare that they have no competing interests.

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