Behavioral Ecology and Sociobiology (2018) 72:151
https://doi.org/10.1007/s00265-018-2568-5

ORIGINAL ARTICLE

Prey naïveté and the anti-predator responses of a vulnerable marsupial prey to known and novel predators

Eleanor C. Saxon-Mills[1] · Katherine Moseby[1,2] · Daniel T. Blumstein[3] · Mike Letnic[1]

Received: 2 February 2018 / Revised: 20 August 2018 / Accepted: 20 August 2018

Abstract

Prey may recognize and respond to predatory cues based on a period of co-evolution or life experience with a predator. When faced with a novel predator, prey may be naïve to the threat posed and/or unable to respond effectively, making them highly susceptible to predation. Burrowing bettongs (*Bettongia lesueur*) are one such species whose naïveté towards introduced predators has contributed to their extinction from mainland Australia. Here, we asked whether bettongs that were predator-naïve and bettongs which had been exposed to feral cats (*Felis catus*) for up to 2 years could discriminate between odors of a predator with which they shared no evolutionary history (feral cats), a predator with which they share a deep evolutionary history (Tasmanian devil—*Sarcophilus harrisii*), a novel herbivore (guinea pig—*Cavia porcellus*), and procedural control (a towel moistened with deionized water). We deployed scents at foraging trays and filmed bettongs' behavior at the trays. Predator-naïve bettongs' latency to approach foraging trays and behavior did not differ between scents. Cat-exposed bettongs increased their latency to approach in the presence of animal scents compared with control, and approached predatory scents slowly and cautiously more often than herbivore and procedural control scents. Taken together, these results suggest that bettongs have not retained anti-predator responses to Tasmanian devils after 8000 years of isolation from mammalian predators but nevertheless show that bettongs exposed to predators are more wary and may be able to generalize predator response using olfactory cues.

Significance statement

When prey encounter a novel predator, they are often naïve to the threat posed and employ ineffective anti-predator responses, because they lack either evolutionary or ontogenetic experience with the predator. Determining how prey identify novel predators is important to improve the success of translocations and reintroductions. Here, we examine how exposure of predator-naïve individual burrowing bettongs to predators influences anti-predator responses. By quantifying bettong responses to odors, we show that those experimentally exposed to cats increased their vigilance in response to odors from cats and Tasmanian devils. The results are consistent with the idea that prey generalize anti-predator responses based on non-specific compounds found in predatory odors, and that exposure to novel predators can improve anti-predator responses.

Keywords Prey naïveté · Anti-predator responses · Olfactory recognition · Generalization · Acquired predator recognition

Introduction

An individual's ability to recognize and respond to predator cues may require periods of co-evolution or ontogeny (life experience) with a predator (Carthey and Blumstein 2018; Parsons et al. 2018). As a result, when a prey encounters a novel predator species, they are often naïve to the threat posed and are unable to recognize or respond effectively (Moseby et al. 2011). Prey naïveté can occur due to isolation from one or more types of predators and this isolation relaxes selection pressure (Blumstein and Daniel 2005). It is also conceivable

Communicated by A. I. Schulte-Hostedde

✉ Eleanor C. Saxon-Mills
eleanorcsaxon@gmail.com

[1] Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

[2] Arid Recovery Ltd., Roxby Downs, SA, Australia

[3] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA

that anti-predator responses could be actively selected against, because the missed opportunity costs to foraging and reproducing from employing anti-predator responses can be high (Brown and Kotler 2004). The loss of anti-predator responses after isolation from predators can occur over very short time periods of time (e.g., as few as 130 years in tammar wallabies—*Macropus eugenii*, Blumstein et al. 2004) and has been attributed to a combination of relaxed selection on anti-predator behaviors and benefits accrued from reducing the energetic costs associated with employing anti-predator behaviors (Caro 2005). However, some species can retain anti-predator responses after extended periods of isolation (e.g., quokkas—*Setonix brachyurus*, after 7000 years of isolation, Blumstein et al. 2001).

Interestingly, the loss of anti-predator responses can be reversed (Griffin et al. 2000). Indeed, prey species have been observed to relearn predatory cues in as little as one generation (moose—*Alces alces*, Berger et al. 2001). Prey may not only relearn lost behaviors, but may also learn to discriminate and respond to novel predators after short periods of coexistence (e.g., 130 years for ringtail possums—*Pseudocheirus peregrinus*, Anson and Dickman 2013; 30 years for Iberian waterfrogs—*Pelophylax perezi*, Nunes et al. 2014).

Whether, and the degree to which, prey are able to learn about their predators is of particular importance when native prey have suffered dramatic declines as a result of predation by introduced predators. For instance, Australia has one of the world's worst mammalian extinction records, with 30 mammals becoming extinct since European settlement (Woinarski et al. 2015). Predation by introduced predators, red foxes and feral cats (*Felis catus*), is cited as one the major factors driving declines of mammal populations (Short and Smith 1994), due in part to prey naïveté. Naïveté towards introduced predators is thought to make native mammals particularly susceptible to predation, given the long history of predator absence during evolution (Moseby et al. 2015a).

Conservation managers have employed various tactics to address the issue of predation by introduced predators. This includes manipulating the environment of prey species by eradicating introduced predators and moving at-risk populations onto predator-free islands and into predator-proof fenced exclosures (Short 2009). However, these methods often are short-term solutions, because predator removal is costly (Parks et al. 2012), and an incursion by a few individual predators can decimate an entire population (Christensen and Burrows 1995). Additionally, this very isolation from predatory threats may exacerbate the problem of prey naïveté, because the removal of predatory threats relaxes selection pressures (Moseby et al. 2015a). Exacerbation of prey naïveté brought about by isolation from predators may be a key factor why many reintroductions, which often use animals from predator-free areas, fail to establish self-sustaining populations (Moseby et al. 2015a).

To combat the problem of prey naïveté, some researchers have attempted to manipulate the traits of prey individuals by training naïve or captive-bred animals to recognize and respond to novel predatory threats prior to reintroduction. In some instances, wildlife managers have used Pavlovian conditioning by pairing predatory cues with an aversive event to stimulate prey learning (McLean et al. 2000; Griffin et al. 2001) Predator learning after training has been demonstrated in a variety of fishes (Ferrari et al. 2007; Brown et al. 2011) and mammals (Griffin et al. 2001). However, few studies have tested whether pre-release training actually improves post-release survival (houbara bustards—*Chlamydotis [undulata] macqueenii*, Van Heezik et al. 1999; Puerto Rican parrots—*Amazona vittata*, White et al. 2005). Moseby et al. (2015b) suggest that pairing predatory cues with non-dangerous aversive events in training assays, such as stimulated capture (Griffin et al. 2001), or being shot at by water pistols (Mclean et al. 1996), may not stimulate the appropriate anti-predator responses to the threat of actual predation. Instead, they propose that in situ exposure to low densities of introduced predators may facilitate prey learning and it may permit natural selection to occur in response to predation.

Another foundational issue in applied predator recognition is the degree to which prey are able to generalize their anti-predator responses from a known predator to an unknown predator (Ferrari et al. 2007). The ability to generalize anti-predator responses from a known to an unknown predator would be particularly advantageous and may reduce prey mortality and enhance survival in environments with novel predators (Ferrari et al. 2007). Generalized responses towards predators have been reported in a variety of taxa, including fish (Brown et al. 2011; Ferrari et al. 2016), reptiles (Webb et al. 2009), and mammals (Griffin et al. 2001; Blumstein et al. 2008).

The archetype hypothesis (Cox and Lima 2006) suggests one mechanism for generalization, where prey can recognize unknown predators that have a close phylogenetic relationship to known predators, and which share similar traits (life history, hunting style, physical appearance). True generalization, however, does not require predators to be of the same archetype; instead, learning about one potential threat heightens responses to other threats (Ferrari et al. 2007). One mechanism for true generalization is the use of chemical compounds to identify predatory odors regardless of previous exposure, termed the common constituents hypothesis (Nolte et al. 1994; Ferrero et al. 2011; Osada et al. 2015).

In this study, we test two hypotheses. First, do burrowing bettongs (*Bettongia lesueur*) with up to 2-year experience living with a novel, introduced predator (feral cats) exhibit wary anti-predator responses in the presence of this predatory odor? Second, do cat-exposed bettongs respond with increased wariness in the presence of unknown predator odors? We tested our hypotheses by exposing cat-exposed and non-cat-exposed bettongs to the scents of two predators, Tasmanian devils (*Sarcophilus harrisii*) and cats, guinea pigs (*Cavia porcellus*) and a procedural control (a towel moistened with deionized water) and analyzing their behavioral responses.

Methods

Study site

We conducted the study at Arid Recovery (30° 29′ S, 136° 53′ E), a 123-km^2 fenced reserve located approximately 20 km north of Roxby Downs, South Australia. Arid Recovery was established in 1997, and currently consists of six separate fenced exclosures, in which introduced predators foxes, cats, and dingoes were systematically removed between 1999 and 2001. Locally extinct mammals were reintroduced between 1998 and 2008, including greater stick-nest rats (*Leporillus conditor*), greater bilbies (*Macrotis lagotis*), burrowing bettongs, and western barred bandicoots (*Perameles bougainville*) (Moseby et al. 2011). We conducted our study in May 2017; at this time, five of the exclosures were predator-free and one, the Red Lake exclosure, had feral cats introduced in 2014 to examine the effects of living with predators on prey behavior and population biology (West et al. 2018). In this study, we used the Red Lake Exclosure (26 km^2) as our predator treatment site and the Northern Expansion (30 km^2) as a control predator-free site.

Study species

Bettongs are social, medium-sized marsupials (1–1.5 kg) that once occupied the widest geographical range of any Australian mammal species. They now occur naturally on only three predator-free offshore islands: Bernier, Dorre, and Barrow Islands (Short and Turner 2000). Bettongs' inability to avoid predation by introduced cats and foxes has been implicated as one of the major causes of their decline (Christensen and Burrows 1995; Moseby et al. 2015b). Three reintroductions to fenced mainland sites have occurred in efforts to conserve the species: Heirisson Prong in 1992 (failed), Arid Recovery in 1999–2001, and Scotia Wildlife Sanctuary in 2008.

The bettongs at Arid Recovery were sourced from the Bernier Island and Heirisson Prong (originally Dorre Island) populations (Moseby et al. 2011). Bernier and Dorre Islands have been almost entirely predator-free since their isolation from the mainland approximately 8000 years ago (Shortridge 1910; Gale 2009), which occurred due to rising sea levels (Lewis et al. 2013). Before this isolation, the range of the bettong overlapped with that of native marsupial predators, including Tasmanian devils, thylacine (*Thylacinus cynocephalus*) (Gale 2009), and western quolls (*Dasyurus geoffroii*) (Shortridge 1910).

There is no documented evidence that Indigenous people lived permanently on these islands, but it is possible that they visited with dingoes during the Holocene (Abbott 1979). Domestic dogs and cats were brought to Dorre and Bernier Islands in the late nineteenth century, when pastoral operations were established, and between 1908 and 1918, when the islands operated as hospitals for Aboriginal people (Shortridge 1910). During this time, dogs were used for mustering livestock, companion pets, and likely helped Aborigines in the hunting of mammals (Stingemore 2010). During the early twentieth century, cats were believed to have hunted mammals on the islands and were thought to be a factor contributing to the rarity of the western barred bandicoot on the islands (Shortridge 1910).

The islands could have been predator-free from as early as 1918, at the closure of the hospital. The islands were considered to be free of mammalian predators in 1959 when a scientific expedition conducted an inventory of the islands' biota (Ride et al. 1962). Thus, the bettongs introduced to Arid Recovery had 8000 years with no exposure to native mammalian predators and only a relatively brief period (maximum 60 years) of co-occurrence with introduced predators (domestic dogs and cats) in modern times, which ended at least 60 years ago.

Experimental rationale

We aimed to examine the response of bettongs to predatory odors that they have ontogenetic experience with and those that are entirely novel, and whether experience with predators leads to an increased wariness around predator odors in general. To do so, we video recorded the behavior of bettongs with different histories of predator exposure at stations where food baits were paired with either a predator or control scent. The olfactory stimuli were sourced from an evolutionary novel introduced predator—cats, a predator with which they share a deep evolutionary history—Tasmanian devils, a novel herbivore scent—guinea pigs, and a control scent (a towel moistened with deionized water).

We chose to test cat stimuli to examine whether bettongs could respond to an evolutionary novel predator after 3-year ontogenetic exposure with the predator. Importantly, from an applied perspective, predation by cats is implicated in the decline of bettongs and the failure of previous reintroductions (Short and Turner 2000). The Tasmanian devil scent was chosen to examine if bettongs can generalize anti-predator responses to an unknown predator after ontogenetic exposure. This is complicated by the shared deep evolutionary history of bettongs and Tasmanian devils. However, if we find that bettongs lost anti-predator responses to Tasmanian devils, then we can examine their ability to generalize anti-predator responses.

To examine prey learning and generalization abilities, we made the following predictions:

> If ontogenetic experience influences bettongs' ability to discriminate amongst predators and non-predators, we expect that cat-exposed bettongs display a heightened anti-predator response to cats compared to herbivore and control scents, and that control bettongs would not discriminate between scents.
>
> If bettongs have lost anti-predator responses to Tasmanian devils after 8000 years of isolation, we would expect that control bettongs do not discriminate between Tasmanian devil and control scents.
>
> If bettongs have lost anti-predator responses to Tasmanian devils, then any heightened response to devil scent in cat-exposed bettongs implies generalization has occurred due to ontogenetic exposure to cats. If bettongs can generalize, we expect that cat-exposed bettongs display a heightened anti-predator response to both cats and devils, and that control bettongs do not discriminate between predator and control scents.

Experimental design

Foraging stations consisted of 100 g of oats evenly distributed in 500-g soil, and then partially buried, since bettongs dig for food (Short and Turner 1993). Scent treatments were attached to stakes and positioned directly behind the food at a distance of 20 cm. The stations were located every 200 m along vehicle tracks, 2 m from the tracks. Bettongs have large home ranges, between 29 and 35 ha dependent on population density (Finlayson and Moseby 2004), so the placement of stations along vehicle tracks should collect videos from a representative sample of the bettong population. The population density of bettongs in 2016 was estimated to be 19.8/km^2 and 61.7/km^2 in Red Lake Exclosure and Northern exclosure respectively (Moseby et al. 2018a, b). A random number generator determined the scent treatment deployed at each station. At each station, a motion sensor, night-vision camera (Bushnell "NatureView", Bushnell "Trophy Cam", or Scoutguard "ZeroGlow") was positioned 1 m high on a stake positioned 2 m away from the food bait. Cameras had a 60° field of view; cameras could monitor the bait from approximately 1 m to the left or right of the station, 1.5 m in front of the bait station, and 2 m behind the bait, depending on visibility. Bettongs' behavior was recorded from when bettong was within 1 m of the station. Cameras were programmed to record 60-s length videos. To reduce the amount of nontarget videos recorded, motion-triggered recording was set to begin 30 min before sunset. A lapse of between 0 and 1 s occurred between consecutive videos, depending on capabilities of the camera model deployed.

To avoid the effects of habituation to foraging stations, each station was setup for one night only. A total of 157 stations in Red Lake Exclosure and 122 stations in Northern Expansion were deployed across nine nights in May 2017. Not all videos were usable because cameras often failed due to insufficient battery life, nontarget species consuming the food before bettongs could forage and/or human error in camera positioning and camera programming. A total of 59 stations in Red Lake Exclosure and 48 stations in Northern Expansion were usable and analyzed by Saxon-Mills.

Stimulus preparation

We used cotton towels imbued with body odor because previous studies have shown that odors sourced from fur and skin presented a more immediate risk of predation compared to odors sourced from feces or urine (Apfelbach et al. 2005; Parsons et al. 2018). Animals used cotton towels as a bedding material for 2 weeks; after which, we cut the towels into 10 × 10-cm pieces, placed them in airtight containers and froze them at − 18 °C until use. We collected guinea pig scents from four different household pets (two male, two female), cat scents from five different household pets (three male, two female), Tasmanian devil scents from two captive bred animals (both male) and a procedural control treatment (control scent): a towel moistened with deionized water before freezing.

Data analysis

In the following data analysis, the two predator-exposure treatments, cat-exposed bettongs, and control group bettongs were analyzed separately. This is because we only had one example of each predator-exposure treatment (our large paddocks). Thus, while individuals with a paddock were replicated, treatments were not formally replicated.

Foraging station avoidance

We compared the number of foraging stations visited and those that were not visited between scent treatments to ask whether bettongs avoided stations based on scent treatment. We used a contingency table to test this hypothesis.

Latency to approach

We calculated the latency to first approach the scent treatment as the duration of time after sunset that the first bettong visited the foraging station. Burrowing bettongs are nocturnal, and are thus active almost exclusively following sunset (Short and Turner 1993), so time after sunset was deemed an

Table 1 Ethogram of burrowing bettongs visiting food baits, indicating the type of behavior and the categories used for analysis

Type	Behavior	Description	Category	Vigilance category
Event	Fast approach	Rapidly hop bipedally towards bait without pausing	Fast approach	Low vigilance
Event	Slow approach	Slow pentapedal movement towards bait, while pausing and looking around	Slow approach	High vigilance
State	Fast escape	Run quickly away from bait	Movement	High vigilance
State	Slow retreat	Move slowly away from bait	Movement	Low vigilance
State	Fast lateral movement	Rapid movement neither towards nor away from bait	Movement	Low vigilance
State	Quadrupedal sniff	On all fours sniffing	Olfactory investigation	High vigilance
State	Bipedal sniff	Stand on back legs sniffing	Olfactory investigation	High vigilance
State	Foraging head down	Head down and feeding	Foraging	Low vigilance
State	Foraging head up	Head up while chewing	Foraging	High vigilance
State	Vigilant interaction with scent	Interacting with scent while sniffing and looking	Olfactory investigation	High vigilance
State	Relaxed interaction with scent	Interacting with scent without sniffing and looking, includes consuming the scent bait	Olfactory investigation	Low vigilance
State	Out of sight	Out of camera range	Other	Other

appropriate analog for latency to investigate. Longer durations before bettongs investigated predatory scents may indicate recognition of a potential threat, or increased wariness or avoidance behaviors (Caro 2005). For latency to approach calculations, we obtained the time of sunset on each day of the experiment at Roxby Downs using an online calculator (Geoscience Australia 2017). We fitted a generalized linear model for each predatory exposure treatment, with scent type as a fixed factor, to test if the latency to approach a foraging station differed between predator and control scents. Because the response variable (duration of time after sunset) was not normally distributed, we $\log10(x)$ transformed the variable prior to analysis. Pairwise comparisons were used to analyze differences in response to scents in predator-exposed and control groups.

Approach events

We scored videos using the event recorder BORIS (Friard and Gamba 2016). To minimize observer bias, blinded methods were used when behavioral data were scored and analyzed. Videos with multiple bettongs present were removed from analysis, to control for the effect that the presence of conspecifics may have on behavior. An ethogram was developed that focused on movement, foraging, and sniffing (Table 1). We scored bettongs' approach behavior as events, either fast approaching or slow approaching. "Fast approach" was defined as when a bettong bipedally hopped towards bait without pausing. "Slow approach" was categorized as slow pentapedal movement towards stations, while pausing and looking around because bettongs, like other macropodids, use their tail and all four limbs when "walking" slowly. We fitted a binomial logistic distribution to investigate if bettongs performed approach behaviors as a function of scent treatment, as bettongs performed either fast or slow approach. Pairwise comparisons were used to analyze differences between responses to scents in predator-exposed and control groups separately. In some instances, approach style was not captured due to delays in camera recording. Recordings that showed neither fast nor slow approaches were removed from this analysis, meaning sample sizes differ from other statistical tests.

Behavioral response to stimuli

After scoring the behaviors of the first minute of a bettong in sight, we calculated the proportion of time in sight allocated to behaviors and combined them into three categories (Table 1). "Olfactory investigation" was comprised of any sniffing behavior, including quadrupedal and bipedal sniffing and olfactory investigation of scent. "Foraging" included both foraging with head raised and foraging with head down. "Movement" included locomotion that occurred following the initial approach, which includes fast lateral movement, fast escape, and slow retreat.

We fitted generalized linear mixed models to investigate if bettongs allocated different amounts of time (proportion of time in sight) to behaviors as a function of scent treatment in each of the two paddocks, separately. We fitted models for the dependent variables, proportion of time in sight engaged in olfactory investigation, foraging, and movement. Because the response variables were not normally distributed and the dataset contained many zero values, we $\log10(x+1)$ transformed each variable prior to analysis. Pairwise comparisons were used to analyze differences between bettongs' responses towards scents in predator-exposed and control groups. Statistical analysis was conducted using IBM SPSS Statistics (IBM corp 2014). We set our alpha to 0.05 for all tests.

Data availability The datasets generated during and analyzed during the current study are available in the Figshare repository, https://doi.org/10.6084/m9.figshare.5649247.v1.

Results

Foraging station avoidance

Neither control group bettongs ($\chi^2 = 1.941$, df = 3, $P = 0.585$) nor cat-exposed bettongs ($\chi^2 = 2.402$, df = 3, $P = 0.493$) avoided foraging stations based on scent treatment type (Table 2).

Latency to approach

Control bettongs did not modify their latency to approach as a function of scent type ($F = 0.198$, df = 3, $P = 0.978$; Fig. 1a). Cat-exposed bettongs modified their latency to approach stations as a function of scent type ($F = 8.112$, df = 3, $P = 0.044$; Fig. 1b). Pairwise comparisons revealed that the latency to approach the unscented control treatment was significantly different from that of cat (Fisher's LSD, $P = 0.006$), guinea pig (Fisher's LSD, $P = 0.045$), and Tasmanian devil (Fisher's LSD, $P = 0.040$) scents, with control scents having a shorter period of latency (Fig. 1b).

Approach behavior

Control group bettongs did not differ in their use of fast and slow approaches across scent treatments ($\chi^2 = 3.683$, df = 3, $P = 0.298$; Fig. 2a). Cat-exposed bettongs showed differences in the proportion of animals engaging in fast or slow approaches between scent treatments ($\chi^2 = 24.583$, df = 3, $P < 0.001$; Fig. 2b). Pairwise comparisons revealed that responses to cat and Tasmanian devil scents differed from control (Fisher's LSD, $P < 0.001$) and guinea pig (Fisher's LSD, $P = 0.001$) scents. A higher proportion of cat-exposed bettongs approached cat and Tasmanian devil scents slowly compared to control and guinea pig scent. Additionally, cat-exposed bettongs only fast approached in the presence of control and guinea pig scent treatments (Fig. 2b).

Behavioral response to stimuli

Both control and cat-exposed bettongs ate from all scent treatments. Control group bettongs did not allocate time differently as a function of scent treatment for olfactory investigation ($F = 0.499$, df = 3, $P = 0919$; Fig. 3a), foraging ($F = 0.671$, df = 3, $P = 0.890$; Fig. 3c), or movement after approach ($F = 2.525$, df = 3, $P = 0.471$; Fig. 3e). Similarly, cat-exposed bettongs showed no difference in the proportion of time spent in olfactory investigation ($F = 1.962$, df = 3, $P = 0.580$; Fig. 3b), foraging ($F = 0.040$, df = 3, $P = 0.998$; Fig. 3d), and movement after approach ($F = 0.105$, df = 3, $P = 0.991$; Fig. 3f) across treatments.

Discussion

Bettongs with no ontogenetic experience with mammalian predators did not discriminate between stations with odors of predators and either stations with odors of herbivores or with the procedural control. These results suggest that predator-naïve bettongs do not respond to predator odors. In contrast, cat-exposed bettongs increased their latency to approach in the presence of predator and herbivore odors but not a procedural control. Bettongs also approached stations slowly and cautiously more often in the presence of predatory odors than the odors of a novel herbivore or a procedural control. These results suggest that cat-exposed bettongs were more wary in the presence of novel odors and assess the odors of predators as threatening. Interestingly, cat-exposed bettongs responded similarly to a predator with which they have exposure too, cats, and one that they have no experience with for the past 8000 years, Tasmanian devils. The employment of anti-predator responses to both cat and Tasmanian devil odors suggests that bettongs have the ability to generalize anti-predator responses amongst at least a subset of their predators.

Cat-exposed bettongs took longer to approach in the presence of animal scents, whereas control bettongs did not alter latency to approach as a function of scent treatment. Greater latency to approach foraging stations with animal scents suggests that cat-exposed bettongs avoid areas with a novel odor, which may be adaptive because it reduces that potential for encountering a high-risk situation. Avoiding areas of risk

Table 2 Counts of foraging stations that were visited and not visited in control and cat-exposed groups. Counts of visited stations reflect stations where videos of bettongs were recorded, and counts of stations not visited represent stations where no videos of bettongs were recorded

	Control group		Cat-exposed group	
Scent treatment	Approached station	No visitation	Approached station	No visitation
Cat	15	3	14	3
Control	20	3	10	7
Guinea pig	13	4	15	6
Tasmanian devil	11	4	9	3

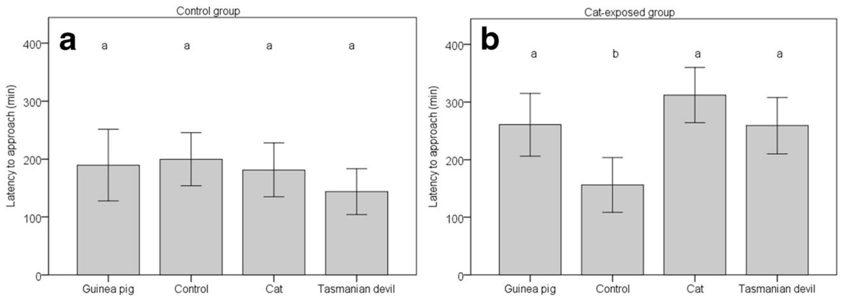

Fig. 1 Average latency to approach stations (minutes after sunset) (± 1 SE) in **a** control (cats $n = 10$, procedural control $n = 14$, guinea pig $n = 9$, and Tasmanian devil $n = 5$) and **b** cat-exposed (cats $n = 14$, procedural control $n = 9$, guinea pig $n = 11$, and Tasmanian devil $n = 8$) bettongs. Similar letters above bars identify statistically indistinguishable ($P > 0.05$) pairwise differences

should have the greatest influence on the outcome of predator-prey interactions, because avoiding predators before direct contact reduces the number of encounters with predators (Lima and Dill 1990).

Many animal species exhibit heightened vigilance in response to predator odors and allocate more time towards sniffing, scanning, and escaping behaviors at the expense of foraging (Caro 2005). Our results provide no evidence that bettongs allocated more time to vigilance activities in response to encountering predator scents once they approached the foraging station. However, cat-exposed bettongs were more likely to approach foraging trays slowly and cautiously in the presence of predators' scents, and only approached quickly in the presence of herbivore and control scents. Such cautious approach may provide bettongs with more time to assess the true risk of predation (FitzGibbon 1994).

Inspecting predatory cues appears counterintuitive for prey, as the risk of predation increases as prey approach predatory threats (Fishman 1999). However, predator inspection can provide benefits to prey species which may include acquiring more information on the nature of the potential threat, informing conspecifics of the potential threat, deterring predator attack, and advertising quality to mates (Parsons et al. 2018). Prey can minimize costs due to lost opportunities to forage and reproduce by inspecting predator cues before employing anti-predator behaviors (Fishman 1999). Our results are consistent with the theory that prey recognize predatory odors and inspect them to acquire more information on the nature of the potential threat (Parsons et al. 2018).

Control bettongs did not inspect or employ other anti-predator responses in the presence of predatory odors including Tasmanian devils, a predator with which they share deep evolutionary history but have been isolated from for 8000 years. These findings suggest that bettongs' isolation from predators has resulted in the loss of anti-predator behavior. Such loss of anti-predatory behavior could be lost due to the absence of selection by predators or indeed be selected against (Blumstein 2002). Populations that occur in predator-free environments often occur at high densities and are limited the availability of food resources (Alder and Levins 1994). In such environments, with intense intra-specific competition for food resources, it is conceivable that anti-predator behaviors may be lost due to strong selection against missed opportunity costs arising from engaging in unnecessary anti-predator behavior (Novosolov et al. 2013).

Cat-exposed bettongs seemingly identified both cats and Tasmanian devils as predatory threats and responded similarly to their odors. Taken together, these findings suggest that the

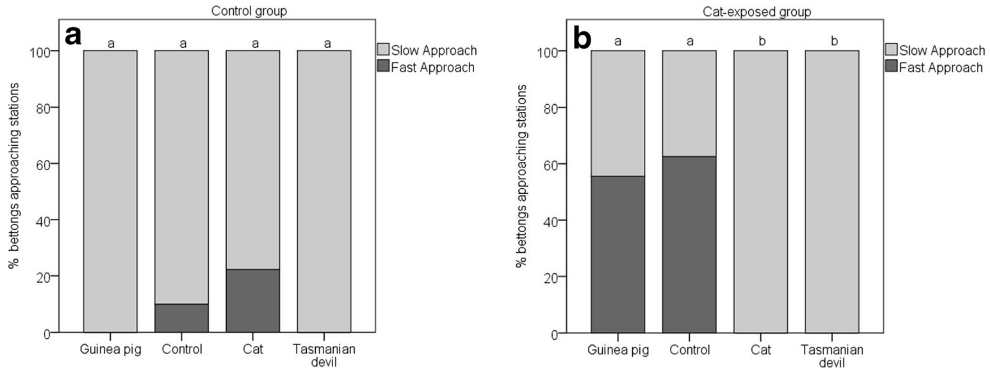

Fig. 2 Proportion of **a** control (cats $n = 9$, procedural control $n = 10$, guinea pig $n = 4$, and Tasmanian devil $n = 3$) and **b** cat-exposed (cats $n = 11$, procedural control $n = 8$, guinea pig $n = 9$, and Tasmanian devil $n = 5$) bettongs engaged in fast and slow approach behaviors in response to the deployment of predatory and control olfactory stimuli. Similar letters (e.g., a and b) above bars identify statistically indistinguishable ($P > 0.05$) pairwise differences

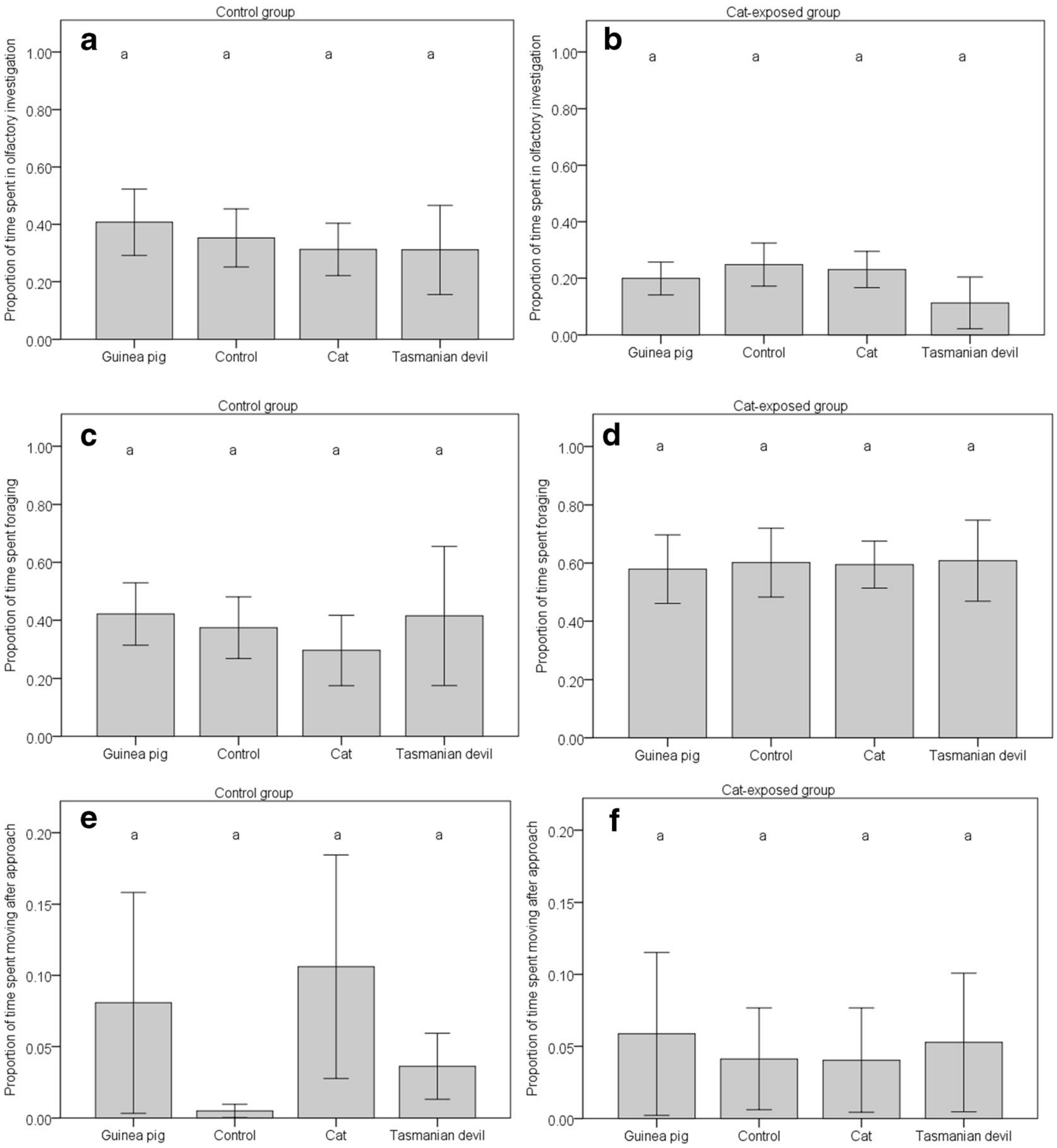

Fig. 3 Average proportion of time (± 1 SE) control (cats $n = 15$, procedural control $n = 20$, guinea pig $n = 13$, and Tasmanian devil $n = 11$) and cat-exposed (cats $n = 14$, procedural control $n = 10$, guinea pig $n = 15$, and Tasmanian devil $n = 9$) bettongs spent engaged in **a**, **b** olfactory investigation, **c**, **d** foraging, and **e**, **f** movement after approach in response to the deployment of predatory and control olfactory stimuli. Similar letters above bars identify statistically indistinguishable ($P > 0.05$) pairwise differences

responses of cat-exposed bettongs to Tasmanian devil scent were due to the generalization of responses from cats to Tasmanian devils, as a result of cat exposure. At a proximate level, this observation is consistent with the "common constituents hypothesis," whereby chemical compounds that are commonly present in predator odors cause prey to respond similarly to known and novel predatory scents (Nolte et al. 1994; Ferrero et al. 2011; Osada et al. 2015). However, the common constituents hypothesis implicitly assumes that this recognition of predatory odors, based on these common constituents, is innate, but control group bettongs did not innately discriminate amongst predatory odors. Therefore, the common constituents hypothesis does not account for the apparent recognition of predatory cues demonstrated by cat-exposed bettongs, as control group bettongs did not innately recognize predatory odors.

Our study has implications for reintroduction of threatened vertebrates because it demonstrates that pre-release exposure to low levels of controlled predation can alter the expression of anti-predator behaviors in predator-naïve prey (Moseby et al. 2015a). Previous studies have shown that development of observable anti-predator behaviors was associated with improved post-release survival of houbara bustards (Van Heezik et al. 1999) but not black-footed ferrets (*Mustela nigripes*, Biggins et al. 1999). However, it is important to note, that our study focused on behavioral responses in the face of potential predatory threats, and thus does not show that exposure to cats actually improves the survival of bettongs reintroduced to predator-rich environments. To do the latter would require conducting releases of cat-exposed and predator-naïve bettongs into a common environment with predators and monitoring their survival. We recommend that further research is conducted to determine if behavioral responses towards predators brought about by predator exposure translate to enhanced survival of reintroduced prey.

Acknowledgments We thank the Arid Recovery staff and volunteers for their help with this study. We thank the two anonymous reviewers whose comments and suggestions helped improve and clarify this manuscript.

Funding Funding for this project was provided by the Australian Research Council.

Compliance with ethical standards

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

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The work was conducted under the UNSW animal ethics (APEC Approval 15/19A) and in accordance with *The Australian Code of Practice for the Care and Use of Animals for Scientific Purposes* (*1997*).

References

Abbott I (1979) Aboriginal man as an exterminator of wallaby and kangaroo populations on islands round Australia. Oecologia 44:347–354

Alder GH, Levins R (1994) The island syndrome in rodent populations. Q Rev Biol 69:473–490

Anson J, Dickman C (2013) Behavioral responses of native prey to disparate predators: naïveté and predator recognition. Oecologia 171:367–377

Apfelbach R, Blanchard CD, Blanchard RJ, Hayes RA, McGregor IS (2005) The effects of predator odors in mammalian prey species: a review of field and laboratory studies. Neurosci Biobehav Rev 29:1123–1144

Berger J, Swenson JE, Persson I (2001) Re-colonising carnivores and naive prey: conservation lessons from Pleistocene extinctions. Science 291:1036–1039

Biggins DE, Vargas A, Godbey JL, Anderson SH (1999) Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*). Biol Conserv 89:121–129

Blumstein DT (2002) Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. J Biogeogr 29:685–692

Blumstein DT, Barrow L, Luterra M (2008) Olfactory predator discrimination in yellow-bellied marmots. Ethology 114:1135–1143

Blumstein DT, Daniel JC (2005) The loss of anti-predator behaviour following isolation on islands. Proc R Soc Lond B 272:1663–1668

Blumstein DT, Daniel JC, Mclean IG (2001) Group size effects in quokkas. Aust J Zool 49:641–649

Blumstein DT, Daniel JC, Springett BP (2004) A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. Ethology 110:919–934

Brown GE, Ferrari MCO, Malka PH, Russo S, Tressider M, Chivers DP (2011) Generalization of predators and nonpredators by juvenile rainbow trout: learning what is and is not a threat. Anim Behav 81:1249–1256

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014

Caro T (2005) Anti-predator defenses in birds and mammals. The University of Chicago Press, Chicago

Carthey AJR, Blumstein DT (2018) Predicting predator recognition in a changing world. Trends Ecol Evol 33:106–115

Christensen P, Burrows N (1995) Project desert dreaming: experimental reintroduction of mammals to the Gibson Desert, Western Australia. In: Armstrong DP, Hayward MW, Moro D, Seddon PJ (eds) Advances in reintroduction biology of Australia and New Zealand Fauna CSIRO Publishing, Clayton South VIC, pp 199–207

Cox JG, Lima SL (2006) Naïveté and an aqautic-terrestrial dichotomy in the effects of introduced predators. Trends Ecol Evol 21:674–680

Ferrari MCO, Crane AL, Chivers DP (2016) Certainty and the cognitive ecology of generalization of predator recognition. Anim Behav 111:207–211

Ferrari MCO, Gonzalo A, Messier F, Chivers DP (2007) Generalisation of learned predator recognition: an experimental test and framework for future studies. Proc R Soc Lond B 274:1853–1859

Ferrero DM, Lemon JK, Fluegge D, Pashkovski SL, Korzan WJ, Datta SR, Spehr M, Fendt M, Liberles SD (2011) Detection and avoidance of a carnivore odor by prey. P Natl Acad Sci USA 108:11235–11240

Finlayson GR, Moseby KE (2004) Managing confined populations: the influence of density on the home range and habitat use of reintroduced burrowing bettongs (*Bettongia lesueur*). Wildlife Res 31:457–463

Fishman MA (1999) Predator inspection: closer approach as a way to improve assessment of potential threats. J Theor Biol 196:225–235

FitzGibbon CD (1994) The costs and benefits of predator inspection behaviour in Thomson's gazelles. Behav Ecol Sociobiol 34:139–148

Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol Evol 7:1324–1330

Gale SJ (2009) Event chronostratigraphy: a high-resolution tool for dating the recent past. Quat Geochronol 4:391–399

Geoscience Australia (2017) Compute sunrise, sunset & twilight times, http://www.ga.gov.au/geodesy/astro/sunrise.jsp

Griffin AS, Blumstein DT, Evans CS (2000) Training captive-bred or translocated animals to avoid predators. Conserv Biol 14:1317–1326

Griffin AS, Evans CS, Blumstein DT (2001) Learning specificity in acquired predator recognition. Anim Behav 62:577–589

IBM corp (2014) IBM SPSS Statistics for Windows, Version 23.0. IBM Corp., Anmonk, NY

Lewis SE, Sloss CR, Murray-Wallace CV, Woodroffe CD, Smithers SG (2013) Post-glacial sea-level changes around the Australian margin: a review. Quat Sci Rev 74:115–138

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

McLean IG, Lundie-Jenkins G, Jarman PJ (1996) Teaching an endangered mammal to recognise predators. Biol Conserv 75:51–62

McLean IG, Schmitt NT, Jarman PJ, Duncan C, Wynne CDL (2000) Learning for life: training marsupials to recognise introduced predators. Behaviour 137:1361–1376

Moseby K, Carthey AJR, Schroeder T (2015a) The influence of predators and prey naivety on reintroduction success: current and future directions. In: Armstrong D, Hayward M, Moro D, Seddon PJ (eds) Advances in reintroduction biology of Australian and New Zealand fauna. CSIRO Publishing, Melbourne, Australia, pp 29–42

Moseby KE, Blumstein DT, Letnic M (2015b) Harnessing natural selection to tackle the problem of prey naïveté. Evol Appl 9:334–343

Moseby KE, Letnic M, Blumstein DT (2018b) Designer prey: can controlled predation accelerate selection for anti-predator traits in naïve populations? Biol Conserv 217:213–221

Moseby KE, Lollback GW, Lynch CE (2018a) Too much of a good thing; successful reintroduction leads to overpopulation in a threatened mammal. Biol Conserv 219:78–88

Moseby KE, Read JL, Paton D, Copley P, Hill BM, Crisp HA (2011) Predation determined the outcome of 10 reintroduction attempts in arid South Australia. Biol Conserv 144:2863–2872

Nolte DL, Mason JR, Epple G, Aronov E, Campbell DL (1994) Why are predator urines aversive to prey? J Chem Ecol 20:1505–1516

Novosolov M, Raia P, Meiri S (2013) The island syndrome in lizards. Glob Ecol Biogeogr 22:184–191

Nunes AL, Orizaola G, Laurila A, Rebelo R (2014) Rapid evolution of constitutive and inducible defenses against an invasive predator. Ecology 95:1520–1530

Osada K, Miyazono S, Kashiwayanagi M (2015) The scent of wolves: pyrazine analogs induce avoidance and vigilance behaviors in prey. Front Neurosci 9:363

Parks H, Clifton K, Best L, Johnson B (2012) Now that we have our pest-proof fence, are we safe or trapped? Pac Conserv Biol 18:77–80

Parsons MH, Apfelbach R, Banks PB, Cameron EZ, Dickman CR, Frank ASK, Jones ME, McGregor IS, McLean S, Müller-Schwarze D, Sparrow EE, Blumstein DT (2018) Biologically meaningful scents: a framework for understanding predator–prey research across disciplines. Biol Rev 93:98–114

Ride WDL, Mees GF, Douglas AM, Royce RD, Tyndale-Biscoe CH (1962) The results of an expedition to Bernier and Dorre Islands, Shark Bay, Western Australia in July 1959. Government Printer, Perth

Short J (2009) The characteristics and success of vertebrate translocations within Australia. Wildl Res and Management Pty Ltd., Kalamandu, WA, Australia

Short J, Smith A (1994) Mammal decline and recovery in Australia. J Mammal 75:288–297

Short J, Turner B (1993) The distribution and abundance of the burrowing bettong (*Marsupialia*: *Macropoidea*). Wildlife Res 20:525–533

Short J, Turner B (2000) Reintroduction of the burrowing bettong *Bettongia lesueur* (*Marsupialia*: *Potoroidae*) to mainland Australia. Biol Conserv 96:185–196

Shortridge GC (1910) Account of the geographical distribution of the marsupials and monotremes of south-west Australia, having special reference to the specimens collected during the Balston expedition of 1904-1907. P Zool Soc Lond 55:803–848

Stingemore JL (2010) Surviving the "cure": life on Bernier and Dorre islands under the lock hospital regime. PhD thesis, University of Western Australia

Van Heezik Y, Seddon PJ, Maloney RF (1999) Helping reintroduced houbara bustards avoid predation: effective anti-predator training and the predictive value of pre-release behaviour. Anim Conserv 2:155–163

Webb JK, Du WG, Pike DA, Shine R (2009) Chemical cues from both dangerous and nondangerous snakes elicit antipredator behaviours from a nocturnal lizard. Anim Behav 77:1471–1478

West R, Letnic M, Blumstein DT, Moseby KE (2018) Predator exposure improves anti-predator responses in a threatened mammal. J Appl Ecol 55:147–156

White THJ, Collazo JA, Vilella FJ (2005) Survival of captive-reared Puerto Rican parrots released in the Caribbean National Forest. Condor 107:424–432

Woinarski JCZ, Burbidge AA, Harrison PL (2015) Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. P Natl Acad Sci USA 112:4531–4540