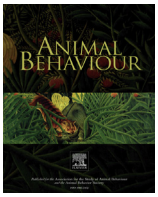
Animal Behaviour 137 (2018) 133–139

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Discrimination of introduced predators by ontogenetically naïve prey scales with duration of shared evolutionary history

Lisa A. Steindler [a], Daniel T. Blumstein [b], Rebecca West [a, c], Katherine E. Moseby [a, c], Mike Letnic [a, *]

[a] Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia
[b] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA
[c] Arid Recovery Ltd., Roxby Downs, Australia

ARTICLE INFO

Article history:
Received 14 August 2017
Initial acceptance 6 November 2017
Final acceptance 27 December 2017

MS. number: 17-00652

Keywords:
antipredator behaviour
evolutionary history
greater bilby
ontogenetic naïveté
predator odour discrimination
prey naiveté hypothesis

Hypotheses on the discrimination and recognition of predators by prey are divided as to whether the prey species' ability to recognize and avoid predators is proportionate to the duration of evolutionary exposure to specific predators or is a result of more generalized discrimination processes. Moreover, understanding of the timeframes necessary for prey species to maintain or acquire appropriate responses to introduced predators is poorly understood. We studied a population of wild, ontogenetically predator naïve greater bilbies, *Macrotis lagotis*, living within a large (60 km^2) predator-free exclosure, to determine whether they modified their burrow-emergence behaviour in response to olfactory stimuli from introduced predators, dogs, *Canis familiaris*, and cats, *Felis catus*. Greater bilbies have shared over 3000 years of coevolutionary history with dogs but less than 200 years with cats. Bilbies spent more time only partially emerged (with at most head and shoulders out) as opposed to fully emerged (standing quadrupedally or bipedally) from their burrows when dog faeces were present, in comparison to faeces of cats, rabbits and an unscented control. Our results were consistent with the 'ghosts of predator past' hypothesis, which postulates that prey species' abilities to respond to the odours of predators scales with their period of coexistence. Our study supports the notion that introduced predators should be regarded as naturalized if prey possess an innate ability to detect their cues and respond accordingly.

Hypotheses on the discrimination and recognition of predators by prey are divided as to whether a prey's ability is proportionate to the duration of coevolution (Banks & Dickman, 2007; Blumstein, 2002) or a result of ontogenetic experience (Berger, 1998) with specific predators, or whether prey simply generalize their response to all predators based on characteristics shared among predators (Apfelbach, Parsons, Soini, & Novotny, 2015; Cox & Lima, 2006). The 'ghosts of predators past' hypothesis (Peckarsky & Penton, 1988) suggests that species that have had a long period of coevolution with a predator may possess 'hard-wired' antipredator responses. Prey may exhibit innate abilities to recognize and respond to the scents and images of coevolved predators (Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005; Blumstein, Daniel, Schnell, Ardron, & Evans, 2002; Monclús, Rödel, Von Holst, & De Miguel, 2005). In contrast, prey species that have not been evolutionarily exposed to predators may learn through ontogenetic experience to recognize and respond to predators' olfactory cues (Anson & Dickman, 2013; Berger, Swenson, & Persson, 2001) or to their visual cues (Atkins et al., 2016).

The 'predator archetype' hypothesis suggests that for many prey species, their capacity to recognize and respond to cues associated with predators may be generalized and not be limited to specific predators (Cox & Lima, 2006). As a result, prey may exhibit antipredator responses towards cues that share characteristics with those with which they have coevolved or cohabited (Cox & Lima, 2006). For example, the 'common constituents' hypothesis posits that odours from predators share common compounds that prey should respond to regardless of the predator that produced it (Apfelbach et al., 2015; Nolte, Mason, Epple, Aronov, & Campbell, 1994). It has also been suggested that a prey's ability to discriminate between predator odours is influenced by its body size (Apfelbach et al., 2015; Woolhouse & Morgan, 1995). Small prey are more likely to encounter predators at close quarters and thus may have little opportunity to assess the threat posed by different

---

[*] Correspondence: M. Letnic, Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, 2035, Sydney, Australia.
E-mail address: m.letnic@unsw.edu.au (M. Letnic).

https://doi.org/10.1016/j.anbehav.2018.01.013
0003-3472/

predators (Apfelbach et al., 2015). Hence smaller, less mobile prey species are predicted to fear almost any carnivore odour (McEvoy, Sinn, & Wapstra, 2008; Nolte et al., 1994).

In situations where the risk of predation is low or nonexistent, the benefits of expressing antipredator behaviours may be outweighed by the costs of missed opportunities to obtain food resources or mates. Consequently, relaxed selection by predators on both ontogenetic and evolutionary timescales may result in ‘prey naïveté’, whereby species may have diminished antipredator behaviour and/or fail to recognize and/or mount effective responses against novel predators (Banks, 1998; Blumstein, 2006; Blumstein, Daniel, & Springett, 2004; Goldthwaite, Coss, & Owings, 1990).

Understanding of the factors that dictate prey species' abilities to recognize and respond to predators is an important theoretical issue (Cox & Lima, 2006; Ferrari, Messier, & Chivers, 2008; Parsons, Apfelbach, Banks, Cameron, Dickman, Frank et al., 2017), as well as an important applied topic. Evolutionary prey naïveté towards introduced predators has been hypothesized to be a major factor contributing to population declines of native prey species and failed attempts to reintroduce locally extinct species (Moseby et al., 2011; Salo, Korpimäki, Banks, Nordström, & Dickman, 2007). However, our understanding of the evolutionary timeframes necessary for prey species to maintain or acquire appropriate responses to introduced predators is poorly known. Many of the studies that have investigated the evolved abilities of wild prey to recognize cues associated with coevolved and novel predator species did not control for variation in ontogenetic exposure to predators (Anson & Dickman, 2013; Carthey & Banks, 2012, 2016). Thus, it remains possible that responses of prey species to predator cues reported in many studies were, to some extent, shaped by generalization (Dickman & Doncaster, 1984) or reflect a result of both an individual's lifetime experience and the history of evolutionary exposure to predators (Blumstein, 2006; Hettena, Munoz, & Blumstein, 2014).

Knowledge of the extent to which prey species' responses to predators are the result of coevolution or learning and the timeframes required for appropriate antipredator responses to be lost or develop has direct application to the development of programmes that attempt to overcome the problem of prey naïveté (Moseby, Blumstein, & Letnic, 2016; West, Letnic, Blumstein, & Moseby, 2017). Indeed, if prey species can adequately recognize and appropriately respond to introduced predators, then it may no longer be necessary to classify them as introduced but instead naturalized (Carthey & Banks, 2012).

Prey are able to detect and respond to the presence of predators through the use of sight, sound and smell (Banks, Bytheway, Carthey, Hughes, & Price, 2014; Parsons, Apfelbach, Banks, Cameron, Dickman, Frank et al., 2017). In coevolved predator–prey systems, prey often use predator odours as cues to detect predators, gauge risk and respond accordingly (Anson & Dickman, 2013; Apfelbach et al., 2005; Apfelbach et al., 2015; Parsons, Apfelbach, Banks, Cameron, Dickman, Frank et al., 2017). Prey use refuges, such as burrows, to avoid predation (Martín & López, 1999; Sih, Petranka, & Kats, 1988). Since predators can move through landscapes, the risk of predation outside burrows fluctuates through time. Consequently, prey must decide when it is safe to move in and out of a refuge (Martín & López, 2015; Parsons, Apfelbach, Banks, Cameron, Dickman, Frank et al., 2017; Sih, 1997). We predicted that if a prey species is able to detect a predator first, then it will optimize the avoidance of predators through appropriate risk assessment strategies (e.g. Lima & Dill, 1990). However, this relies on a prey's ability to rapidly recognize and discriminate between predator cues.

Here we evaluated the ideas that a prey's ability to respond to predator odours is influenced by the duration of coevolution, as opposed to a generalized response to shared characteristics of predator cues. We did this by quantifying the behavioural responses of an ontogenetically predator naïve population of wild-living greater bilbies, *Macrotis lagotis*, to faecal samples from two introduced predators (dog, *Canis familiaris*, and cat, *Felis catus*), a herbivore (rabbit, *Oryctolagus cuniculus*) and a procedural control (no odour). Bilbies have shared varying periods of coevolution with these predators and rabbits. Dingoes/dogs and feral cats are both known to predate on bilbies, and have been implicated in previous reintroduction failures of bilbies beyond predator-free fenced reserves (Moseby et al., 2011; Southgate & Possingham, 1995). Since many mammalian predators scent mark features in the landscape, such as the burrows of prey species, by depositing urinary and faecal odours (Corbett, 1995; Gorman & Trowbridge, 1989), we deployed faeces at the entrance of bilbies' burrows. The decision to emerge from a refuge, such as a burrow, requires prey to estimate predation risk outside the shelter versus the benefits of potential rewards (Martín & López, 1999; Sih, 1997).

If the duration of coevolution with predators influenced bilbies' ability to respond to predators, we would expect that bilbies should be more wary when emerging from burrows when dog rather than cat faeces are present. Bilbies have had more than 3000 years of coevolution with dogs/dingoes (Savolainen, Leitner, Wilton, Matisoo-Smith, & Lundeberg, 2004), but less than 200 years of coevolution with cats (Abbott, 2002). If bilbies generalized their response to placental predators, we expected that bilbies would respond similarly to dogs and cats, but not respond to rabbits or the control (no faeces). Rabbits are an introduced herbivore, harmless to bilbies, with which bilbies have had less than 160 years historical exposure (Zenger, Richardson, & Vachot-Griffin, 2003). We restricted our test to introduced predators to which the source populations would have been exposed in the 20th century and did not include the scent of a marsupial predator, the western quoll, *Dasyurus geoffroii*, with which they would have had a longer period of evolutionary coexistence. The reasons for not including quoll scent were twofold. First, quolls and bilbies have not coexisted in the wild for over 100 years (Morris et al., 2003) and second, it was not possible for us to obtain scent samples from captive quolls at the time the study was conducted. Even though we did not have scents of a marsupial predator, we are confident that our test of the hypothesis, that the duration of coevolution with a predator influences predator recognition, was not confounded by ontogenetic experience, as the population of bilbies within our study site have not been exposed to placental predators for more than 16 years.

METHODS

Study Area

We studied bilbies within the 60 km^2 fenced exclosure at Arid Recovery Reserve, South Australia (12 300 ha, 30°29′S, 136°53′E). Arid Recovery Reserve is in the arid zone, with an average rainfall of 149.4 mm (from 1997 and 2015; Bureau of Meteorology, 2015). A 1.8 m high predator-proof fence surrounds the reserve. Dingoes, foxes, cats and rabbits are absent from the fenced exclosures where the study was undertaken. Locally extinct mammals, including bilbies, were reintroduced to the Arid Recovery Reserve in 2000 following the eradication of predators and introduced feral herbivores, such as rabbits (Moseby, Hill, & Read, 2009). All the mammals reintroduced to Arid Recovery are wild, as they are not given supplementary food and are exposed to avian and reptilian predators.

Study Species

Greater bilbies are an omnivorous, burrowing, nocturnal and largely solitary marsupial (Moseby, Cameron, & Crisp, 2012). Male bilbies weigh 800–2500 g and females weigh 600–1200 g (Southgate, Christie, & Bellchambers, 2000). The distribution of bilbies has contracted markedly since European settlement of Australia in 1788 and they now occupy just 20% of their former range (Southgate, 1990). This decline has been attributed primarily to predation by introduced red foxes, *Vulpes vulpes*, and feral cats (Moseby & O'Donnell, 2003; Southgate, 1990), as well as dingoes/wild dogs (Pavey, 2006). Naïveté towards introduced predators (such as feral cats and red foxes) has been implicated in the decline of many Australian mammals (Moseby et al., 2012). Bilbies have been successfully reintroduced to some areas and islands within their former range where feral cats and foxes are absent, intensively controlled or eradicated (Moseby & O'Donnell, 2003).

The reintroduced population of bilbies at Arid Recovery Reserve were sourced from captive stock from Monarto Zoo (Moseby & O'Donnell, 2003), which descended from wild individuals captured from deserts in Western Australia and the Northern Territory (Moseby et al., 2011). Bilbies can produce a litter of one to three young, four times a year, and have a captive longevity of 5–9 years (Southgate et al., 2000). Based on the reproductive rate of the bilby and historical source of the population of bilbies at Arid Recovery, we assumed that this population, in the wild, has gone through five predator-naïve generations over the past 16 years.

Sources and Storage of Treatment Odours

We used faeces from three species: domestic dogs, domestic cats and wild rabbits along with a procedural control, which was no faeces present. We used domestic dog scats as previous studies have shown that they are chemically indistinguishable from those of dingoes (Carthey, 2013). To overcome the issue of decomposition of faecal odours after deposition, domestic dog and cat faecal samples were collected immediately from private pet owners and local veterinary hospitals, stored and sealed in airtight zip lock bags, and frozen at minus 20 °C (Carthey, 2013). Wild rabbit faecal samples were collected fresh from rabbit warrens. Disposable gloves were always worn when handling faeces to prevent cross contamination of odours. As faecal samples were collected from private pet owners and local veterinary hospitals, from multiple individual sources, the total number of donor individuals was unknown; however, it may be approximated that samples were sourced from between two and 10 separate individuals of each species. As rabbit faeces were collected from a wild population, the number of source individuals is unknown. To take potential donor effects into account, faeces allocation was randomized. Since the diets of domestic pets were consistent between individuals and were made up of a mix of raw meats and pet foods, we did not consider diet to be a potential confounding source in analysis (Carthey, 2013).

Bilby Burrow Emergence Behaviour

A total of 18 wild individual bilbies (10 females, eight males) were caught and fitted with a 9 g core tail mount with whip antenna radiotransmitter (Sirtrack, Havelock North, New Zealand) between August and October 2015. Transmitters were attached according to the protocol of the South Australian National Parks and Wildlife Service (Moseby & O'Donnell, 2003). Individuals were radiotracked daily to their diurnal burrows for 2–8 weeks, with experiments commencing at least 2 nights after transmitter attachment.

We used a repeated measures design in which each individual was presented with each odour treatment once according to a predetermined balanced order. We controlled for order effects experimentally and assessed these effects statistically.

Odour treatments were presented on every third night of tracking, for a single night. There were two 'baseline' nights, where no odour was presented, to ensure that there was no residual odour from the previous treatment. Faeces were presented on the surface of the ground, within 20 cm of the burrow entrance. If there were multiple burrow entrances, faeces were placed at the burrow entrance that recorded the strongest VHF transmitter signal. One piece of cat and dog faeces of similar size and weight (approximately 25–30 g) and 20 pellets of rabbit faeces were presented outside the burrow accordingly.

At each burrow entrance on treatment and 'baseline' nights a metal post was positioned approximately 1–2 m from the burrow entrance, supporting either a Bushnell Trophy Cam (Bushnell, Overland Park, KS, U.S.A.), Scoutguard SG550V or Scoutguard Zeroglow (Scoutguard, Molendinar, Australia), infrared motion sensor video camera. Cameras were mounted 20–100 cm off the ground and were programmed to take 60 s of video, when triggered, to enable species identification and observe burrow emergence and behavioural responses to the odour treatments (Fig. 1), with a 0 s interval between possible triggers, from dusk until dawn (1700–0700 hours).

Behavioural Scoring

We constructed an ethogram of behaviours (Table 1) based upon the initial observations of experimental videos. All behaviours were treated as mutually exclusive (Blumstein & Daniel, 2007). We scored video recordings ≥60 s using the event recorder JWatcher (Blumstein & Daniel, 2007). We focused on quantifying only the first 60 s video footage of each bilby at the burrow entrance. We did this because our study focused on quantifying bilbies' initial

Figure 1. Experimental set-up for the bilby predator odour discrimination study. The photo shows the infrared motion sensor video camera mounted on a metal post outside the burrow entrance of a radiotracked bilby.

Table 1
Ethogram of greater bilby, *M. lagotis*, burrow emergence behaviour

Behaviour	Description of behaviour
Partially emerged	Individual at burrow entrance, with at most head and shoulders out. Head fixated, potentially looking or sniffing or looking and sniffing
Fully emerged	Individual standing quadrupedally or bipedally, fully emerged from burrow. Head fixated, potentially looking or sniffing, or looking and sniffing
Walk	Animal moving slowly when exiting and fully emerged from burrow
Run	Animal moving rapidly when exiting and fully emerged from burrow
Out of sight in burrow	Individual seen on camera and retreated out of sight into burrow

behavioural responses to the presence of predators' scats and we wanted to eliminate the potential for our observations to be influenced by habituation to the presence of scats. We calculated the proportion of time in sight allocated to each behaviour. We quantified the behaviour of both identified bilbies (i.e. those with a tail transmitter), as well as other individuals that shared the burrows with marked subjects. Behavioural scoring of the videos commenced at the start of each 60 s video, with comparisons only made between 'treatment' nights. The inclusion of 'no odour' treatments ensured we were able to compare behavioural responses to the different odour treatments and as such we did not compare 'baseline' and 'treatment' nights.

For analysis we combined behaviours in which the bilby was fully emerged from the burrow to create a new category 'fully emerged' (Table 1). It was not possible to record data blind because our study involved focal animals in the field and it was possible to visually identify the odour treatments.

Analysis of Behavioural Data

We fitted a series of linear mixed-effects models in SPSS-22 (IBM Corp., Armonk, NY, U.S.A.) with diagonal error structure to test bilby burrow emergence behaviour in response to treatment. We had two fixed effects in our models: treatment and presentation order. To account for the possibility of nonindependence between observations, we included individuals as a random effect. In preliminary analyses, we also tested for the effects of moon phase; as this was never significant, however, we did not include it as a predictor variable in our final model. In no case was presentation order significant; we retained it as a blocking factor in the analysis, however, to control for its effect statistically (Quinn & Keough, 2002). In instances where the treatment effect was significant ($P < 0.05$), we used Fisher's least significant difference (LSD) post hoc test to examine planned comparisons for differences in response to each odour.

Ethical Note

Work was conducted under animal ethics APEC Approval Number 1/2014 'Tackling Prey Naivety in Australia's Threatened Mammals' and in accordance with the South Australian Wildlife Ethics Committee.

Bilbies were captured with either cage traps (45 × 20 cm and 20 cm high), baited with a combination of peanut butter and rolled oats, or hand-held fishing nets as described by Moseby et al. (2012). As bilbies did not readily enter the cage traps, 17 of 18 bilbies were captured with nets. Bilbies that were netted were located during night-time searches conducted with spotlights from a vehicle. When sighted, they were approached and netted with a hand-held net. On capture, bilbies were transferred from the net to a dark nylon fleece bag for processing and transmitter attachment. Bilbies were securely restrained within the processing bag, rather than anaesthetized during the attachment of the radiotransmitter. The transmitter weighed 1.25% of an 800 g female and 0.07% of a 1400 g male bilby.

For transmitter attachment, hair on the tail of the bilby was removed using scissors and disposable razors, and a transmitter attached using Leukoplast adhesive tape. To prevent the formation of tail ulcers, extra care was taken to ensure that the transmitter was not firmly pressed to the tail (Moseby & O'Donnell, 2003). Only trained personnel were responsible for transmitter attachment.

To ensure that animal movements were not hindered by the capture and processing procedure, daily radiotracking of individuals commenced immediately after transmitter attachment. For 15 bilbies, the tail transmitters fell off after approximately 2–3 months. For three bilbies, the transmitters did not fall off and were manually removed. These bilbies were captured by placing cage traps near their burrows within a temporary pen constructed of wire netting (Southgate, McRae, & Atherton, 1995). The bilbies were restrained as described above and the transmitters removed by cutting the tape with scissors. Each of the bilbies was deemed healthy on release; however, further checks were not possible because we could not locate individual bilbies without transmitters.

RESULTS

There was no effect of treatment on the proportion of time that bilbies spent out of sight in the burrow ($F_{3,\ 29.836} = 0.036$, $P = 0.991$; Fig. 2a), walking ($F_{3,\ 34.225} = 0.634$, $P = 0.598$; Fig. 2b) and running ($F_{3,\ 11.195} = 1.054$, $P = 0.407$; Fig. 2c).

There was a significant effect of treatment on the proportion of time that bilbies spent partially emerged from their burrows, with at most their head and shoulders exposed ($F_{3,\ 34.389} = 5.974$, $P = 0.002$; Fig. 2d). Planned comparisons (Fig. 2d) revealed that bilbies spent more time partially emerged when dog faeces were present compared to cat faeces (Fisher's LSD, dog versus cat: $P = 0.013$), rabbit faeces (Fisher's LSD, dog versus rabbit: $P = 0.015$) and the control (no faeces; Fisher's LSD, dog versus control: $P \leq 0.001$). There were no significant differences in time spent partially emerged when cat and rabbit faeces (Fisher's LSD, cat versus rabbit: $P = 0.922$), cat faeces and the control (Fisher's LSD, cat versus control: $P = 0.135$), and rabbit faeces and the control were present (Fisher's LSD, rabbit versus control: $P = 0.213$; Fig. 2d).

There was a significant effect of treatment on the combined proportion of time spent fully emerged ($F_{3,\ 32.283} = 3.134$, $P = 0.039$; Fig. 2e). Bilbies spent less time fully emerged from the burrow when dog faeces were present compared to the control (no faeces; Fisher's LSD, dog versus control: $P = 0.006$; Fig. 2e). There was no significant difference between time spent fully emerged when dog faeces were present compared to cat faeces (Fisher's LSD, dog versus cat: $P = 0.180$) and rabbit faeces (Fisher's LSD, dog versus rabbit: $P = 0.078$). There were no differences in the time spent fully emerged when cat and rabbit faeces (Fisher's LSD, cat versus rabbit: $P = 0.676$), cat faeces and the control (Fisher's LSD, cat versus control: $P = 0.184$), and rabbit faeces and the control were present (Fisher's LSD, rabbit versus control: $P = 0.407$; Fig. 2e).

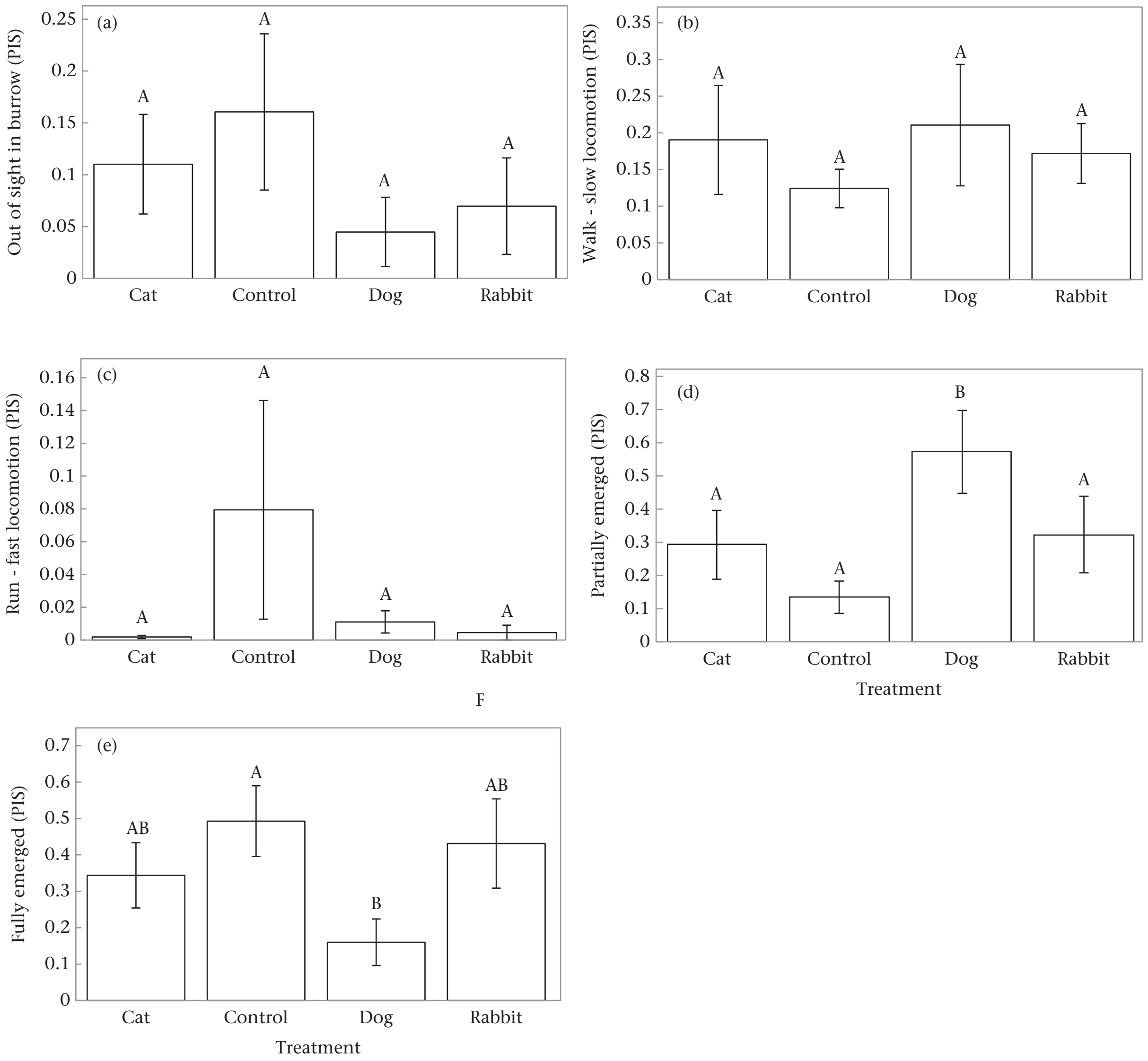


Figure 2. The mean (±1 SEM) proportion of time in sight (PIS) that bilbies allocated to burrow emergence behaviours (a) out of sight in burrow, (b) walk, i.e. slow locomotion, (c) run, i.e. fast locomotion, (d) partially emerged and (e) fully emerged. Similar letters above bars identify pairwise differences that are not statistically distinguishable ($P > 0.05$).

DISCUSSION

Our results provide support for the ‘ghosts of predators past’ hypothesis (Peckarsky & Penton, 1988) which posits that prey species' ability to respond to predator cues scales with the duration of their coevolution. This finding was evidenced by the greater proportion of time that bilbies spent partially emerged from the burrow as opposed to fully emerged, when dog faeces were present. In contrast, bilbies spent proportionately more time fully emerged from their burrows when cat (an introduced predator) and rabbit faeces (an introduced herbivore) and the procedural control (no odour) were presented. Despite complete ontogenetic naïveté and at least 16 years of evolutionary isolation, bilbies at the Arid Recovery Reserve appear to have retained specific antipredator responses towards the olfactory cues of dogs/dingoes, but have a negligible response to cats. Bilbies have shared over 3000 years of evolutionary history with dogs/dingoes, compared to cats with which they have had less than 200 years of evolutionary exposure. Our results support the idea that in coevolved predator–prey systems, prey may possess innate abilities to detect the risk associated with predator cues and respond accordingly, but lack this form of recognition when predators are novel (Banks et al., 2014; Zhang, Zhao, Zhang, Messenger, & Wang, 2015).

Our results showed that, while partially emerged, bilbies appeared to discriminate between the odours of dogs and cats. They similarly showed a weak response to the odours of cats, harmless rabbits and the unscented control, while partially emerged. These results contradict the ‘predator archetype’ hypothesis, which suggests prey may exhibit a generalized response towards predator cues that share characteristics with their coevolved predators (Cox & Lima, 2006). Our results further contradict the ‘common constituents’ hypothesis, which suggests that odours from placental predators share common sulphur- and nitrogen-rich compounds that prey should respond to regardless of the predator that produced it (Apfelbach et al., 2015; Nolte et al., 1994). These findings further suggest that bilbies responded most to the predator with which they have shared the longest period of coevolution, rather than displaying a generalized response to predator odours.

Bilbies spent the greatest proportion of time partially emerged and the least amount of time fully emerged from the burrow when dog faeces were present. This finding may be due to bilbies making a trade-off between costs and benefits of staying within or leaving their refuges. Predator evasion is often costly in terms of time and energy. Thus, theory predicts that prey individuals should not flee or seek shelter immediately when they detect a predator, but instead should adjust their response according to the level of threat perceived (Ydenberg & Dill, 1986). Many animals modify their refuge use and burrow emergence behaviour according to the estimated levels of predation risk (Martín & López, 1999; Sih et al., 1988; Sparrow, Parsons, & Blumstein, 2016). However, animals require information to make such decisions (Bouskila & Blumstein, 1992). As such, by allocating more time to assessing the potential risks associated with the presence of dog faeces, while in the safety of their burrow entrances, bilbies may have reduced the potential for lethal encounters with a dog/dingo outside their burrow.

Our certainty regarding lifetime predator experiences in this study gave us unique insight into the influence of selection pressure in the retention and development of antipredator behaviours. We know the evolutionary history of predator exposure of the bilby population at Arid Recovery Reserve. We also know that these bilbies have had no ontogenetic exposure to mammalian predators. This is in contrast to most other studies of free-ranging wildlife in which history of predator exposure is unknown. A study of wild bush rats, *Rattus fuscipes*, a species suspected to coexist with free-ranging dogs, showed they had no aversion to dog faecal odours; however, it was acknowledged that the risk posed to rodents by feral dogs in the study area was unknown (Banks, Nelika, Hughes, & Rose, 2002).

There has been little research into when an introduced predator may be considered naturalized. Carthey and Banks (2012) proposed that introduced predators should be considered native predators when their prey species are no longer naïve towards them. That bilbies with no lifetime exposure to mammalian predators appear to possess an innate ability to discriminate and respond to dog/dingo scent by being more reluctant to leave their burrows thus supports the idea that dingoes should be regarded as naturalized (Carthey & Banks, 2012; Frank, Carthey, & Banks, 2016). In contrast to their response to dog faeces, bilbies spent more time fully emerged and less time partially emerged from their burrows in the presence of cat faeces, rabbit faeces and the unscented control. This finding implies that bilbies are naïve towards cats and that less than 200 years of evolutionary exposure to cats may not be long enough for bilbies to develop and retain appropriate predator discrimination abilities (Frank et al., 2016). Like the study by Frank et al. (2016), our study raises the question of how long is long enough before a novel predator, such as a feral cat, may be considered naturalized? In theory, this question could be answered by evaluating the magnitude of native prey's responses to introduced predator cues at many different locations and using time since predator arrival as a predictor variable. Finally, our finding that bilbies have limited ability to discriminate cat scent is also of great applied interest as it better defines the problem that reintroduction programmes of predator-naïve populations face. That is, native Australian mammals in the critical weight range (Burbidge & McKenzie, 1989) facing entirely novel predators may not be able to identify them as a threat.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.20tq5.

Acknowledgments

We thank local pet owners and the Roxby Downs Vet Clinic—Whyalla Vet for the supply of odours and the Arid Recovery staff and many volunteers for their assistance with the study. This research was funded by the Australian Research Council (ARC-Linkage Grant (no. LP130100173) to M.L., K.M. and D.T.B.) and Holsworth Wildlife Research Endowment (RG152215) (to L.S and M.L).

References

Abbott, I. (2002). Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. *Wildlife Research, 29*(1), 51–74. https://doi.org/10.1071/WR01011.

Anson, J. R., & Dickman, C. R. (2013). Behavioral responses of native prey to disparate predators: Naiveté and predator recognition. *Oecologia, 171*(2), 367–377. https://doi.org/10.1007/s00442-012-2424-7.

Apfelbach, R., Blanchard, C. D., Blanchard, R. J., Hayes, R. A., & McGregor, I. S. (2005). The effects of predator odors in mammalian prey species: A review of field and laboratory studies. *Neuroscience & Biobehavioral Reviews, 29*(8), 1123–1144. https://doi.org/10.1016/j.neubiorev.2005.05.005.

Apfelbach, R., Parsons, M. H., Soini, H. A., & Novotny, M. V. (2015). Are single odorous components of a predator sufficient to elicit defensive behaviors in prey species? *Frontiers in Neuroscience, 9*(263). https://doi.org/10.3389/fnins.2015.00263.

Atkins, R., Blumstein, D. T., Moseby, K. E., West, R., Hyatt, M., & Letnic, M. (2016). Deep evolutionary experience explains mammalian responses to predators. *Behavioral Ecology and Sociobiology, 70*(10), 1–9. https://doi.org/10.1007/s00265-016-2181-4.

Banks, P. B. (1998). Responses of Australian Bush Rats, *Rattus fuscipes*, to the odor of introduced *Vulpes vulpes*. *Journal of Mammalogy, 79*(4), 1260–1264. https://doi.org/10.2307/1383017.

Banks, P. B., Bytheway, J. P., Carthey, A. J., Hughes, N. K., & Price, C. J. (2014). Olfaction and predator-prey interactions amongst mammals in Australia. In A. Glen, & C. R. Dickman (Eds.), *Carnivores of Australia: past, present and future* (pp. 389–412). Collingwood, Australia: CSIRO Publishing.

Banks, P. B., & Dickman, C. R. (2007). Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology & Evolution, 22*(5), 229–230. https://doi.org/10.1016/j.tree.2007.02.006.

Banks, P., Nelika, K., Hughes, A., & Rose, T. (2002). Do native Australian small mammals avoid faeces of domestic dogs? Responses of *Rattus fuscipes* and *Antechinus stuartii*. *Australian Zoologist, 32*(3), 406–409. https://doi.org/10.7882/AZ.2002.018.

Berger, J. (1998). Future prey: Some consequences of the loss and restoration of large carnivores. *Behavioral Ecology and Conservation Biology*, 80–100.

Berger, J., Swenson, J. E., & Persson, I. L. (2001). Recolonizing carnivores and naïve prey: Conservation lessons from pleistocene extinctions. *Science, 291*(5506), 1036–1039. https://doi.org/10.1126/science.1056466.

Blumstein, D. T. (2002). Moving to suburbia: Ontogenetic and evolutionary consequences of life on predator-free islands. *Journal of Biogeography, 29*(5–6), 685–692. https://doi.org/10.1046/j.1365-2699.2002.00717.x.

Blumstein, D. T. (2006). The multipredator hypothesis and the evolutionary persistence of antipredator behavior. *Ethology, 112*(3), 209–217. https://doi.org/10.1111/j.1439-0310.2006.01209.x.

Blumstein, D. T., & Daniel, J. C. (2007). *Quantifying Behaviour the JWatcher Way*. Sunderland, MA: Sinauer.

Blumstein, D. T., Daniel, J. C., Schnell, M. R., Ardron, J. G., & Evans, C. S. (2002). Antipredator behaviour of red-necked pademelons: A factor contributing to species survival? *Animal Conservation, 5*(4), 325–331. https://doi.org/10.1017/S1367943002004080.

Blumstein, D. T., Daniel, J. C., & Springett, B. P. (2004). A test of the multi-predator hypothesis: Rapid loss of antipredator behavior after 130 years of isolation. *Ethology, 110*(11), 919–934. https://doi.org/10.1111/j.1439-0310.2004.01033.x.

Bouskila, A., & Blumstein, D. T. (1992). Rules of thumb for predation hazard assessment: Predictions from a dynamic model. *American Naturalist, 139*(1), 161–176. https://doi.org/10.1086/285318.

Burbidge, A. A., & McKenzie, N. L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: Causes and conservation implications. *Biological Conservation, 50*(1–4), 143–198.

Bureau of Meteorology, A. G. (2015). *Mean rainfall (mm) for for Roxby Downs, South Australia, years 1997 to 2015*. Retrieved from http://www.bom.gov.au/climate/data.

Carthey, A. J. (2013). *Naiveté, novelty and native status: Mismatched ecological interactions in the Australian environment*. PhD Thesis. Sydney, Australia: University of Sydney.

Carthey, A. J., & Banks, P. B. (2012). When does an alien become a native species? A vulnerable native mammal recognizes and responds to its long-term alien predator. *PLoS One, 7*(2), e31804. https://doi.org/10.1371/journal.pone.0031804.

Carthey, A. J., & Banks, P. B. (2016). Naiveté is not forever: Responses of a vulnerable native rodent to its long term alien predators. *Oikos, 125*(7). https://doi.org/10.1111/oik.02723.

Corbett, L. K. (1995). *Dingo in Australia and Asia*. Sydney, Australia: University of New South Wales Press.

Cox, J. G., & Lima, S. L. (2006). Naiveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution, 21*(12), 674–680. https://doi.org/10.1016/j.tree.2006.07.011.

Dickman, C. R., & Doncaster, C. P. (1984). Responses of small mammals to Red fox (*Vulpes vulpes*) odour. *Journal of Zoology, 204*(4), 521–531. https://doi.org/10.1111/j.1469-7998.1984.tb02384.x.

Ferrari, M. C., Messier, F., & Chivers, D. P. (2008). Can prey exhibit threat-sensitive generalization of predator recognition? Extending the predator recognition continuum hypothesis. *Proceedings of the Royal Society of London B: Biological Sciences, 275*(1644), 1811–1816. https://doi.org/10.1098/rspb.2008.0305.

Frank, A. S. K., Carthey, A. J. R., & Banks, P. B. (2016). Does historical coexistence with dingoes explain current avoidance of domestic dogs? Island bandicoots are naïve to dogs, unlike their mainland counterparts. *PLoS One, 11*(9), e0161447. https://doi.org/10.1371/journal.pone.0161447.

Goldthwaite, R. O., Coss, R. G., & Owings, D. H. (1990). Evolutionary dissipation of an antisnake system: Differential behavior by California and arctic ground squirrels in above- and below-ground contexts. *Behaviour, 112*(3/4), 246–269. https://doi.org/10.1163/156853990X00220.

Gorman, M. L., & Trowbridge, B. J. (1989). The role of odor in the social lives of carnivores. In J. L. Gittleman (Ed.), *Carnivore Behaviour, Ecology, and Evolution* (pp. 57–88). Springer US.

Hettena, A. M., Munoz, N., & Blumstein, D. T. (2014). Prey responses to predator's sounds: A review and empirical study. *Ethology, 120*(5), 427–452. https://doi.org/10.1111/eth.12219.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology, 68*(4), 619–640. https://doi.org/10.1139/z90-092.

Martín, J., & López, P. (1999). When to come out from a refuge: Risk-sensitive and state-dependent decisions in an alpine lizard. *Behavioral Ecology, 10*(5), 487–492. https://doi.org/10.1655/07-083R2.1.

Martín, J., & López, P. (2015). Hiding time in refuge. In W. E. Cooper, Jr., & D. T. Blumstein (Eds.), *Escaping from predators: an integrative view of escape decisions* (pp. 227–262). Cambridge, U.K.: Cambridge University Press.

McEvoy, J., Sinn, D. L., & Wapstra, E. (2008). Know thy enemy: Behavioural response of a native mammal (*Rattus lutreolus velutinus*) to predators of different coexistence histories. *Austral Ecology, 33*(7), 922–931. https://doi.org/10.1111/j.1442-9993.2008.01863.x.

Monclús, R., Rödel, H. G., Von Holst, D., & De Miguel, J. (2005). Behavioural and physiological responses of naïve European rabbits to predator odour. *Animal Behaviour, 70*(4), 753–761. https://doi.org/10.1016/j.anbehav.2004.12.019.

Morris, K., Johnson, B., Orell, P., Gaikhorst, G., Wayne, A., & Moro, D. (2003). Recovery of the threatened chuditch (*Dasyurus geoffroii*): A case study. In M. Jones, M. Archer, & C. Dickman (Eds.), *Predators with pouches: the biology of carnivorous marsupials* (pp. 435–451). Clayton, Australia: CSIRO Publishing.

Moseby, K. E., Blumstein, D. T., & Letnic, M. (2016). Harnessing natural selection to tackle the problem of prey naïveté. *Evolutionary applications, 9*(2), 334–343. https://doi.org/10.1111/eva.12332.

Moseby, K. E., Cameron, A., & Crisp, H. A. (2012). Can predator avoidance training improve reintroduction outcomes for the greater bilby in arid Australia? *Animal Behaviour, 83*(4), 1011–1021. https://doi.org/10.1016/j.anbehav.2012.01.023.

Moseby, K. E., Hill, B. M., & Read, J. L. (2009). Arid Recovery – A comparison of reptile and small mammal populations inside and outside a large rabbit, cat and fox-proof exclosure in arid South Australia. *Austral Ecology, 34*(2), 156–169. https://doi.org/10.1111/j.1442-9993.2008.01916.x.

Moseby, K. E., & O'Donnell, E. (2003). Reintroduction of the greater bilby, *Macrotis lagotis* (Reid) (marsupialia : Thylacomyidae), to northern South Australia: Survival, ecology and notes on reintroduction protocols. *Wildlife Research, 30*(1), 15–27. https://doi.org/10.1071/WR02012.

Moseby, K. E., Read, J. L., Paton, D. C., Copley, P., Hill, B. M., & Crisp, H. A. (2011). Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation, 144*(12), 2863–2872. https://doi.org/10.1016/j.biocon.2011.08.003.

Nolte, D. L., Mason, J. R., Epple, G., Aronov, E., & Campbell, D. L. (1994). Why are predator urines aversive to prey? *Journal of Chemical Ecology, 20*(7), 1505–1516.

Parsons, M. H., Apfelbach, R., Banks, P. B., Cameron, E. Z., Dickman, C. R., Frank, A. S., et al. (2018). Biologically meaningful scents: A framework for understanding predator–prey research across disciplines. *Biological Reviews, 93*(1), 98–114. https://doi.org/10.1111/brv.12334.

Pavey, C. (2006). *National recovery plan for the greater bilby* Macrotis lagotis. *Northern Territory Department of Natural Resources, Environment and the Arts*. Retrieved from http://www.environment.gov.au/biodiversity/threatened/recovery-plans/national-recovery-plan-greater-bilby-macrotis-lagotis.

Peckarsky, B. L., & Penton, M. A. (1988). Why do *Ephemerella* nymphs scorpion posture: A 'ghost of predation past'? *Oikos, 53*(2), 185–193. https://doi.org/10.2307/3566061.

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge, U.K.: Cambridge University Press.

Salo, P., Korpimäki, E., Banks, P. B., Nordström, M., & Dickman, C. R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B: Biological Sciences, 274*(1615), 1237–1243. https://doi.org/10.1098/rspb.2006.0444.

Savolainen, P., Leitner, T., Wilton, A. N., Matisoo-Smith, E., & Lundeberg, J. (2004). A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Sciences of the United States of America, 101*(33), 12387–12390. https://doi.org/10.1073/pnas.0401814101.

Sih, A. (1997). To hide or not to hide? Refuge use in a fluctuating environment. *Trends in Ecology & Evolution, 12*(10), 375–376. https://doi.org/10.1016/S0169-5347(97)87376-4.

Sih, A., Petranka, J. W., & Kats, L. B. (1988). The dynamics of prey refuge use: A model and tests with sunfish and salamander larvae. *American Naturalist, 132*(4), 463–483. https://doi.org/10.1086/284865.

Southgate, R. (1990). Distribution and abundance of the greater bilby *Macrotis lagotis* Reid (Marsupialia: Peramelidae). In J. H. Seeback, P. R. Brown, R. I. Wallis, & C. M. Kemper (Eds.), *Bandicoots and bilbies* (pp. 293–302). Sydney, Australia: Surrey Beatty.

Southgate, R., Christie, P., & Bellchambers, K. (2000). Breeding biology of captive, reintroduced and wild greater bilbies, *Macrotis lagotis* (Marsupialia: Peramelidae). *Wildlife Research, 27*(6), 621–628. https://doi.org/10.1071/WR99104.

Southgate, R., McRae, P., & Atherton, R. (1995). Trapping techniques and a pen design for the greater bilby *Macrotis lagotis*. *Australian Mammalogy, 18*, 101–104.

Southgate, R., & Possingham, H. (1995). Modelling the reintroduction of the greater bilby *Macrotis lagotis* using the metapopulation model analysis of the likelihood of extinction (ALEX). *Biological Conservation, 73*(2), 151–160.

Sparrow, E. E., Parsons, M. H., & Blumstein, D. T. (2016). Novel use for a predator scent: Preliminary data suggest that wombats avoid recolonising collapsed burrows following application of dingo scent. *Australian Journal of Zoology, 64*(3), 192–197. https://doi.org/10.1071/ZO15068.

West, R., Letnic, M., Blumstein, D. T., & Moseby, K. E. (2017). Predator exposure improves anti-predator responses in a threatened mammal. *Journal of Applied Ecology, 0*(0), 1–10. https://doi.org/10.1111/1365-2664.12947.

Woolhouse, A. D., & Morgan, D. R. (1995). An evaluation of repellents to suppress browsing by possums. *Journal of Chemical Ecology, 21*(10), 1571–1583. https://doi.org/10.1007/BF02035153.

Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior, 16*, 229–249. https://doi.org/10.1016/S0065-3454(08)60192-8.

Zenger, K. R., Richardson, B. J., & Vachot-Griffin, A. M. (2003). A rapid population expansion retains genetic diversity within European rabbits in Australia. *Molecular Ecology, 12*(3), 789–794. https://doi.org/10.1046/j.1365-294X.2003.01759.x.

Zhang, F., Zhao, J., Zhang, Y., Messenger, K., & Wang, Y. (2015). Antipredator behavioral responses of native and exotic tadpoles to novel predator. *Asian Herpetological Research, 6*(1), 51–58. https://doi.org/10.16373/j.cnki.ahr.140023.