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Research article

Prey responses to foxes are not determined by nativeness

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Introduced predators are thought to be responsible for the decline and extinction of their native prey. The prey naivety hypothesis provides a mechanism for these declines, suggesting that native prey are vulnerable to introduced predators as their coevolutionary history is insufficiently long for antipredator behaviours to fully develop. The prey naivety hypothesis thus predicts that prey will be less responsive to introduced predators than to native predators. Australia's endemic small mammals are thought to be vulnerable to predation by red foxes because they are less responsive to – or naive of – a predator with whom they have only co-occurred since the 19th century. To test whether nativeness determines antipredator behaviours we compared small mammal behavioural responses to fox scent outside (Australia) and inside the foxes' native range (North America and Israel). We conducted giving-up density experiments in the deserts of these three regions and evaluated small mammal antipredator responses to fox scent. To place these results in a broader context, we then integrated our results into a global meta-analysis of studies assessing prey responsiveness to fox scent. All small mammals similarly increased their vigilance in response to fox scent, regardless of their coevolutionary history with foxes. Australian small mammals responded with greater wariness to fox scent, by decreasing time at food patches in response to fox scent more than Israeli and American small mammals did. However, we found no evidence that this behaviour influenced foraging as nut consumption was unaffected. Our meta-analysis revealed that globally, small mammals respond with similar wariness to fox scent regardless of whether foxes are their native predator. We found no evidence that

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Australian small mammals respond in a maladaptive manner, compared to the foxes' native prey. Our results suggest that animals can develop antipredator behaviours to introduced predators to the same magnitude as native prey.

Keywords: antipredator behaviour, coordinated distribution experiment, invasive species, macrobehaviour, prey naivety, rapid evolution, *Vulpes*

'*The wise do not let themselves be tricked a second time*'
  The Old Rat, Aesop's Fables

Introduction

Introduced predators are considered key drivers of the decline and extinction of their native prey (Doherty et al. 2016). This notion is founded on the idea that lengthy periods of reciprocal coevolution are necessary for stable species interactions (Carthey and Banks 2014). A lack of coevolutionary history between predators and prey is the key mechanism that ties introduced predators to the decline of their native prey and is known as the prey naivety hypothesis. The prey naivety hypothesis predicts that prey fail to recognise or respond appropriately to introduced predators (Sih et al. 2010). Naivety of prey to introduced predators has been cited as a leading cause of decline of native species globally (Salo et al. 2007, Ross et al. 2019, Anton et al. 2020).

It has been proposed that naivety should be understood in more nuanced ways, beyond a binary of whether or not they recognise introduced predators. Prey might be able to recognise predators but fail to respond appropriately or effectively (Banks and Dickman 2007, Carthey and Blumstein 2018). Banks and Dickman (2007) offered that naivety might be best understood as a scale with four levels. Level 1 naivety represents prey that do not recognise introduced predators as a threat. Level 2 describes prey that respond inappropriately to introduced predators, such as freezing in response to a scent-hunting predator (Hughes et al. 2010). Level 3 describes prey who ineffectively respond to introduced predators, such as attempting to 'out-run' cursorial predators (Carthey and Blumstein 2018). Finally, level 4 naïve prey may respond excessively to the cues of predation, responding with higher levels of vigilance than required, resulting in the loss of foraging opportunities. This framing of prey naivety posits that antipredator behaviours commonly employed to evade native predators might be ineffective at evading introduced predators or maladaptive resulting in the loss of foraging opportunities. Comparisons of small mammal responses outside and inside of a predators native range may allow for the identification of any absent, inappropriate, ineffective, or excessive antipredator behaviours that have developed since predator introduction. To date, no single study has directly compared the behavioural responses of prey outside and inside of their predator's native range to identify whether antipredator responses differ.

Australian red foxes *Vulpes vulpes* are one introduced predator long highlighted as a prominent example of introduced mammalian mesopredators causing the extinction of endemic vertebrate prey (Dickman 1996). Woinarski et al. (2015) attributed the extinction of 13 mammals and the decline of another 45 mammals to red fox predation; and the contributors to the International Union for the Conservation of Nature (IUCN) red list attributed the extinction of 1 bird and 10 small mammals, and the decline of another 9 birds and 28 small mammals, to red foxes (Doherty et al. 2016). Several lines of evidence support the claim that foxes drive extinctions in Australia. Foxes hunt small animals, including threatened native species, and they likely hunted extinct species as well (Stobo-Wilson et al. 2021). Moreover, many of Australia's extinct mammals are within the typical prey range of foxes (Cardillo and Bromham 2001). Foxes were the primary cause of death of (fox-inexperienced) bettongs (*Bettongia penicillata* and *B. lesueur*) released from captivity (Short and Turner 2000, Priddel and Wheeler 2004), and three potoroo species *Potoroidae* went extinct approximately 10 years after foxes established in parts of New South Wales (Short 1998). Finally, poison-baiting programs targeting foxes in Western Australia were associated with increased abundance of 11 mammals (Kinnear et al. 1998, 2002). Such assessments and case studies have earned the red fox a place on the IUCN's 100 of the World's Worst Invasive Alien Species list (Lowe et al. 2000).

Australia's endemic mammals have long been described as naïve towards introduced predators (Banks 1998). A lack of coevolutionary history between introduced predators and Australian small mammals is thought to have exacerbated predation rates (Bytheway and Banks 2019, Steindler et al. 2020, Moseby et al. 2023) and driven small mammal decline and extinction (Salo et al. 2007, Banks et al. 2018, Meyer et al. 2021). Prey naivety towards foxes has been tested by contrasting the behavioural responses of prey to the olfactory, visual, or auditory cues of introduced and native predators. In contradiction with the prey naivety hypothesis, the available evidence shows that Australia's small mammals are just as likely to recognise foxes as they are to recognise their native predators (Carthey and Banks 2016, Banks et al. 2018). Despite this, the prey naivety hypothesis remains the primary proposed mechanism for fox-driven decline and extinction in Australia (Banks et al. 2018, Bytheway and Banks 2019, Steindler et al. 2020, Meyer et al. 2021). Foxes are ecologically and evolutionarily dissimilar from Australia's native predators (Luo et al. 2011), and so it is possible that antipredator behaviours that are effective for native predators are ineffective for foxes. A macroecological analysis of predator recognition patterns in the foxes' global prey may aid in understanding whether Australian small mammals possess any maladaptive antipredator behaviours compared to the foxes native prey (Keith et al. 2023).

Here, we tested for differences in the antipredator strategies of prey to introduced predators by comparing the behavioural responses of small mammals to the scent of foxes outside and inside the foxes' native range. The *Vulpes* genus is considered native throughout Europe, North America, the Middle East and Asia. The genus includes the red fox, the world's most widely distributed terrestrial carnivore (Macdonald and Reynolds 2004), which was introduced to Australia in the early 19th century (Dickman 1996). We conducted the first continentally replicated experiment testing prey responses to predation risk, which enabled us to explicitly test whether Australian small mammal responses to the scent of foxes (outside the foxes' native range) differ from responses of Israeli and North American small mammals (inside the foxes' native range). Further, to determine whether our findings are comparable to studies conducted only inside or only outside the foxes' native range we integrated our results into a global meta-analysis of wild, fox-sympatric, small mammal responses to foxes. The prey naivety hypothesis predicts that small mammal wariness responses should be determined by the nativeness of their predator, with small mammals failing to recognise, or responding inappropriately, ineffectively, or excessively to introduced predators.

Material and methods

Field experiments

We compared the behavioural responses of small mammals to fox scent where foxes are introduced (Australia) and where they are native (Israel and North America). All study sites were in desert systems where apex predators were present, and all predators protected (Table 1). In Australia, study sites were in the Painted Desert, South Australia, and the Simpson Desert, Northern Territory; in Israel two study sites were in

the Arava Valley; and in North America two study sites were in Death Valley National Park, California.

The Painted Desert study site was located at Evelyn Downs, a 2300 km² cattle station. The area receives 160 mm of rain annually and is characterised by *Acacia* woodlands, chenopod shrublands and *Eucalyptus* species along ephemeral creek lines. Predators have been protected since ~ 2012, when the property adopted a non-lethal 'wildlife friendly' approach (Wooster et al. 2019). Foxes and small mammals have been sympatric for 108 years in The Painted Desert. Field work was conducted at the Painted Desert in June 2018. The Simpson Desert study site is a ~ 7000 km² protected area. All predators are protected. The area receives 125 mm of rain annually, and the vegetation community generally consists of drought resistant shrubs, featuring *Zygochloa* and spinifex shrublands. Water is sparsely distributed at both study sites, in the form of natural springs, and human-made dams and bores. The mammalian predator community at both study sites consists of red foxes, cats and dingoes *Canis dingo*. Foxes and small mammals have been sympatric for 104 years in The Simpson Desert. Field work was conducted in the Simpson Desert in August 2019.

The Arava Valley encompasses a section of the Israel–Jordan border. Our study sites were located in the Shezaf and Shahaq Nature Reserves, on the Israeli side. The Arava Valley is a hyper-arid desert receiving 40–60 mm of rain annually. The vegetation community consists of *Vachellia* and *Ziziphus* woodlands. Water is sparsely distributed across the study sites and features a mix of natural springs, artificial dams, troughs and irrigation. The area contains small agricultural villages and fields of intensive crop and dairy farming surrounding nature reserves. The local predator community consists of Arabian wolves *C. lupus arabs*, golden jackals *C. aureus*, red foxes, wild cats *Felis silvestris*, all of whom are protected (Bonsen et al. 2022) and native. Predators are protected from human persecution by law in Israel. Foxes and their small mammal prey coevolved across Israel meaning they have

Table 1. Study species and common predators at the global study sites. Study species lists the small mammals who participated in the giving up density experiments, based on identification from camera traps. Predators present lists the large mammalian predators the occur at each of the study sites from Grinnell (1937), Wooster et al. (2021) and Bonsen et al. (2022). Asterix indicates the scent used to simulate predation risk.

Country (fox native range)	Region	Study species (no. of trays species were observed at)	Predators present	Herbivore scent control
Australia (outside)	Painted Desert, South Australia	*Notomys alexis* (11)	*Canis dingo*	*Bos taurus*
	Simpson Desert, Northern Territory	*Pseudomys hermannsbugensis* (31) *Sminthopsis crassicaudata* (9)	*Vulpes vulpes** *Felis catus*	*Camelus dromedarius*
Israel (inside)	Shezaf Reserve, Arava	*Acomys alexis* (22) *Psamommys obesus* (3) *Gerbillus spp.* (24)	*C. lupus* *C. aureus* *V. Vulpes**	*Bos taurus*
	Shahaq Reserve, Arava		*F. silvestris*	
North America (inside)	Butte Valley, Death Valley National Park, California	*Dipodomys merriami* (40)	*Puma concolor*	*Equus asinus*
	Saline Valley, Death Valley National Park, California	*Peromyscus maniculatus* (15)	*C. latrans*	
			V. macrotis* *Urocyon cinereoargenteus*	

likely been sympatric for more than 10 000 years. Field work was conducted in Israel in November 2018.

The North American study site was located in Death Valley National Park. We conducted our experiments at two study sites, Butte Valley and Saline Valley. Death Valley National Park is the largest protected area in the continental United States and is a hyper-arid desert receiving 25–50 mm of rain annually. The area is characterised by Mojave Desert scrub vegetation. The mammalian predator community consists of mountain lions *Puma concolor*, coyotes *C. latrans*, gray foxes *Urocyon cinereoargenteus* and kit foxes *V. macrotis*. All predators are protected (Lundgren et al. 2022). Foxes and their small mammal prey coevolved in Death Valley meaning they have likely been sympatric for more than 10 000 years. Death Valley field work was conducted in October 2019.

To assess the responses of small mammals to fox scent, we set up giving-up density (GUD) experiments (Brown 1988) at each of the study sites. GUD experiments aim to measure how animals balance the energetic benefits and predation risks of foraging (Brown et al. 1999, Bedoya-Perez et al. 2013). The experiments involve offering a food resource under varying conditions of risk (e.g. distance from cover or predator scent cue) and measuring the quantity of food consumed. Animals foraging at food patches should quit searching for food when predation risk outweighs the benefits of foraging (Pyke 1984). As the food resource is intermixed into a nonedible matrix, time investment to continue foraging increases as consumption occurs. Thus, the amount of food consumed at food patches should be lower at trays that animals perceive the riskiest. GUD experiments have been the primary method used to test the prey naivety hypothesis, most commonly simulating predation risk with the use of predator scent, although other cues have been used (Banks et al. 2018). We used this methodology solely to document the number of food items eaten by small mammals at food patches.

At each study site we set up 30–40 food patches, of which 16–38 had small mammal activity, per site. Food patches were initially set a minimum of 200 m apart along dirt roads. However, in the Australian study site this method proved unfeasible due to the lower densities of small mammals. In Australia we were thus forced to set up the food patches on small mammal tracks ~ 100 m apart. This may have resulted in our Australian sample having fewer individuals than our other field sites. Each food patch was filled with 30 peanut fragments mixed into two litres of sand. A Bushnell MKII or Browning Dark Ops Pro camera collecting video were pointed at each food patch. The number of nuts placed in the trays was increased by 10 nuts if small mammals consumed all of the nuts given. All food patches were placed within 5 m of vegetation, to eliminate cover availability as a variable across our study sites.

Each session included a period of two acclimatisation days, two baseline days, and two experiment days in which a single fox scat or a local herbivore dung was placed within 5 cm of the outside corner of the food patch. Baseline days served as a baseline for response variables (behaviours) to which experiment days were compared. We used scats as the scent source, rather than urine or other body odours, as it is the most commonly used odour in the literature to test for prey naivety (Wallach et al. 2022). Trays were included in the analysis if small mammals attended during both the baseline and experimental period. In Australia and Israel, we used scats of the red fox. In Death Valley, North America, there are no red foxes, but there are kit foxes and gray foxes. We chose to use the scats of kit foxes to keep to the *Vulpes* genus. We used local herbivore scats as a control for predator scent (Table 1) as it provides a pungent animal odour of a local non-threatening animal. We did not use a procedural control (i.e. a rock at a food patch) as it is both uncommon in the literature and would reduce our sample size.

In Australia scats were sourced from four female and three male foxes at Sydney Fox and Dingo Rescue; in Israel the scats were sourced from two female and one male fox at Ramat Gan Safari park; and in North America, scats were sourced from a single male fox from the Orange County Zoo. All foxes were fed on a mix of commercial dog food, rodents, or meat. Fox scats were frozen immediately after collection at −20°C. Scats were kept frozen until they were placed at food patches, within a month of collection. Herbivore scats were collected fresh (moist) from the field, and frozen immediately at −20°C.

Nuts were replenished daily, and we recorded the number of nut fragments consumed at each food patch daily. We analysed the small mammal behaviours at the food patches recorded on the camera traps. We identified the key behaviours at the food patches as vigilance, foraging, autogrooming, locomotion, and engaging in social behaviour, and we measured the time spent at the food patch. However, autogrooming and social behaviour were excluded due to low sample sizes. Time spent foraging was also excluded as we regularly observed small mammals removing seeds to consume them elsewhere or cache them for later, resulting in time spent in this behaviour being a poor indication of antipredator behaviour. This was particularly pronounced in *Gerbillus* species in Israel who stuffed their cheeks with multiple peanut fragments before fleeing. We also observed North American small mammals foraging on donkey scat. We instead use the number of nuts consumed as our metric of foraging, which is a more robust metric, particularly when comparing global small mammals with distinct foraging morphologies (Bedoya-Perez et al. 2013) and included overall time spent at the food patch which represents total time spent exposed to predation risk (Smith et al. 2020). We used a modified version of an ethogram provided by Carthey and Banks (2016), as it has been previously used to test for prey naivety (detailed ethogram in Supporting information). Behaviour was scored by E. I. F. Wooster, A. Geisler-Eide and two volunteers. We calculated the difference in the proportion of time spent before (baseline) and after (experiment) application of the scent, and then compared the difference between behaviours at fox and herbivore scented trays. This made the food patches the replicates in our experiment. We filtered out prey species who were present at fewer than ten trays.. Trays were treated as the replicates in an attempt to control for the

individual differences in small mammal behaviour, however, it was not possible to identify individuals at each food patch, so it is possible the same individuals appeared on more than one tray. This may be more pronounced in Australia where food patches were closer together.

We tested whether time spent in each of the behaviours was influenced by the addition of fox scat, relative to the herbivore scat. We tested whether small mammal responses to fox scent varied according to whether the fox was a native or introduced predator and by the genus of the small mammals observed (as we were not always able to identify small mammals to the species level). We tested our hypotheses using linear mixed effect models in the R package 'lme4' ver. 1.1-23 (www.r-project.org), treating study site and genus as random effects, fox nativeness, scent treatment and their interaction as predictor variables against four response variables (the proportion of time spent vigilant, time spent at food patch, time spent locomoting and nut consumption). The model testing nut consumption was run only with site as a random variable as identifying which species ate which peanuts was not possible. For some behavioural variables, attempting to include genus as a mixed or fixed effect led to issues with model singularity, in these cases, genus was run as a separate model and is presented in the Supporting information. We log-transformed the response variables where necessary to approximate normality, adding a constant to make values non-zero.

Meta-analysis

We conducted a meta-analysis including our results from our field study, to test the generality of our findings. We used the data on fox studies included in the meta-analysis by Wallach et al. (2022), which explores the determinants of predator recognition in prey globally. This database was comparable to our field study because it was focused on small mammals (< 2 kg), included only experiments conducted under free-ranging conditions sympatric with foxes, and on small mammals that had been born locally. Our study sites were distinct from papers in the dataset, in that we focused exclusively on desert landscapes where predators were protected. We filtered the dataset of Wallach et al. (2022) to include only predation risk experiments where a *Vulpes* species was the predator. Including our field data, this left us with a final dataset of 19 studies comprising 80 experiments. This covered 27 small mammal prey species (12 outside and 15 inside of the foxes native range). The majority of studies were conducted in Australia (10 studies), followed by North America (4 studies), Spain (4 studies) and Israel (1 study) (Supporting information). Each study compared the responses of small mammals to the scent of foxes and a control. These studies used four key experimental methodologies; activity, flight initiation distance, giving-up density, and trapping. They measured three small mammal response variables toward fox scent and a control: activity rates,
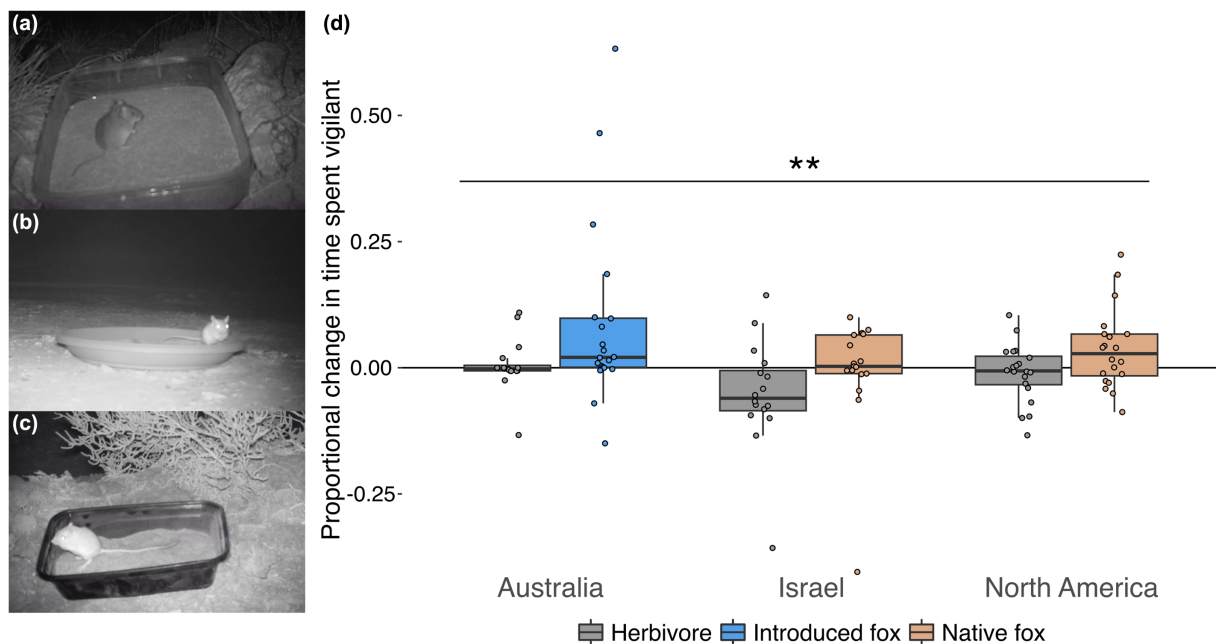

Figure 1. Time small mammals spent vigilant in response to the addition of fox and herbivore scent at food patches. Examples of vigilance behaviours by a small mammal from each country: (a) *Pseudomys hermannsbugensis* in the Painted Desert, Australia; (b) *Gerbillus* spp. in the Arava, Israel; and (c) *Dipodomys merriami* in Death Valley, North America. (d) Both outside (introduced) and inside (native) of the foxes' native range, small mammals spent more time vigilant in response to fox scent compared to herbivore scent. Horizontal line indicates no change between baseline days and experimental days (pre versus post scent placement). Asterisks indicate a statistically significant difference at p < 0.05 between the change in vigilance after the addition of fox scent relative to change in response to herbivore scent treatments. Fox scents were *V. vulpes* in Australia and Israel, and *V. macrotis* in North America. Herbivore scents were camel *Camelus dromedarius* in the Simpson Desert (Australia), cow *Bos taurus* in the Painted Desert (Australia) and Arava (Israel), and donkey *Equus asinus* in Death Valley (North America).
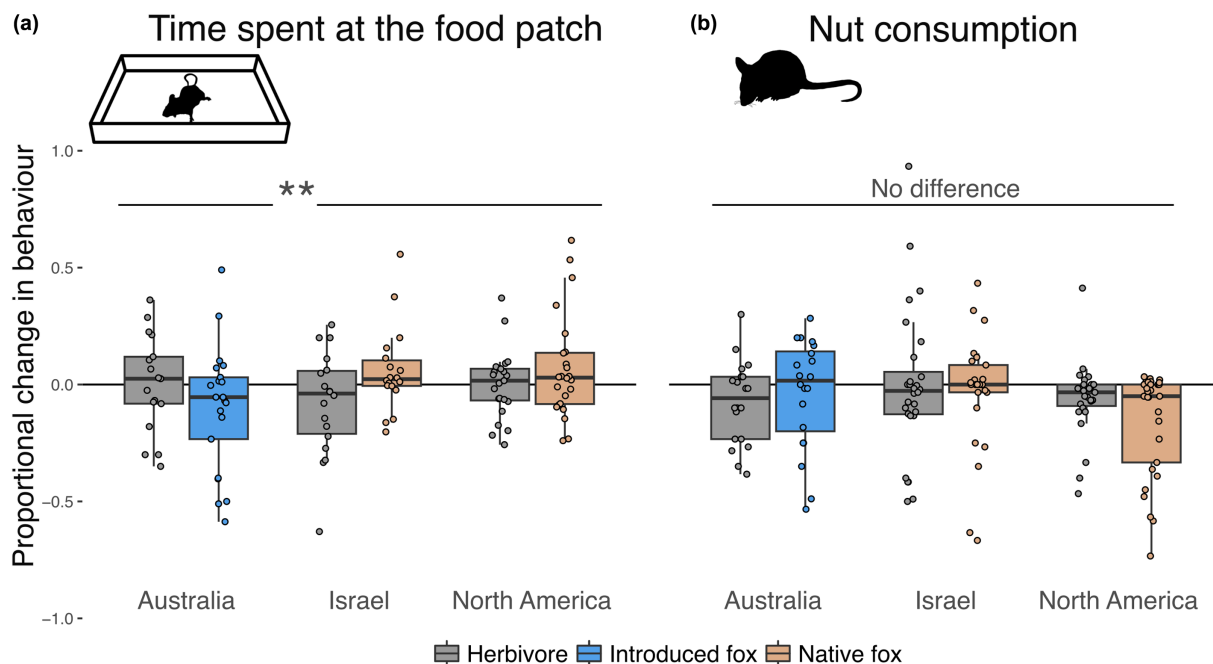
Figure 2. Small mammal time at food patches and nut consumption in response to fox scent relative to herbivore scent. (a) Australian small mammals (outside foxes' native range) reduced time at food patches in response to fox scent relative to herbivore scent. In contrast, Israeli and North American small mammals (inside foxes' native range) increased time at food patches in response to fox scent relative to herbivore scent. (b) Small mammals did not alter nut consumption in response to fox scent relative to herbivore scent in any region. Horizontal line indicates no change between baseline days and experimental days (pre versus post scent placement). Asterisks indicate a statistically significant difference at p < 0.05 between the change in wariness after the addition of fox scent treatments relative to herbivore scent treatments, with line groupings indicating the difference between the regions. Fox scents were *V. vulpes* in Australia and Israel, and *V. macrotis* in North America. Herbivore scents were camel *Camelus dromedarius* in the Simpson Desert (Australia), cow *Bos taurus* in the Painted Desert (Australia) and Arava (Israel), and donkey *Equus asinus* in Death Valley (North America).

wariness behaviours (i.e. vigilance) and foraging rates (i.e. food consumption before and after the addition of scent).

Using the Hedge's g effect sizes of the small mammals' responses to fox scent from the Wallach et al. (2022) database, we constructed a random-effects meta-analytic model testing whether small mammal responses to fox scent could be predicted by fox nativeness. Modelling was undertaken using the function *rma.mv* in the R package 'metafor' (ver. 2.4-0, www.r-project.org), with study as a random effect. Random-effects meta-analytic models weigh the influence of each data point by sampling variance, thus accounting for discrepancies in data quality.

Results

Field experiments

Small mammals increased the proportion of time they spent vigilant in response to fox scent relative to herbivore scent (linear mixed effects model; $\chi^2 = 7.53$, p = 0.006; Fig. 1d). There was no difference in time spent vigilant in response to fox scent outside and inside of the foxes' historic native range ($\chi^2 = 2.12$, p = 0.145, interaction: $\chi^2 = 0.32$, p = 0.57).

Australian small mammals decreased time at food patches in response to fox scent relative to herbivore scent, while Israeli and North American small mammals increased time spent (interaction: $\chi^2 = 6.7$, p = 0.009; Fig. 2a). Neither scent treatment ($\chi^2 = 0.44$, p = 0.51) nor nativeness ($\chi^2 = 0.57$, p = 0.45) influenced time spent at the food patch on their own. However, this difference between time allocation strategies did not carry over to influence foraging behaviour. The addition of fox scent had no effect on nut consumption rates ($\chi^2 = 0.86$, p = 0.35; Fig. 1b) either outside or inside of the fox's historic native range ($\chi^2 = 0.05$, p = 0.82, interaction: $\chi^2 = 1.36$, p = 0.24; Fig. 2b). No other behaviours were influenced by fox scent, fox nativeness, nor their interaction (Supporting information).

Meta-analysis

Placing our results within a meta-analysis of 80 experiments of 27 small mammal species responding to fox scent (fox native predator n = 39; introduced predator n = 41), we found that small mammals responded to *Vulpes* scent regardless of whether they were the foxes' native prey (z = 2.4, p = 0.0151) or not (z = 3.66, p = 0.0002, Fig. 3, Supporting information), with no difference in the strength of response (post hoc test: z = 1.78, p = 0.08).
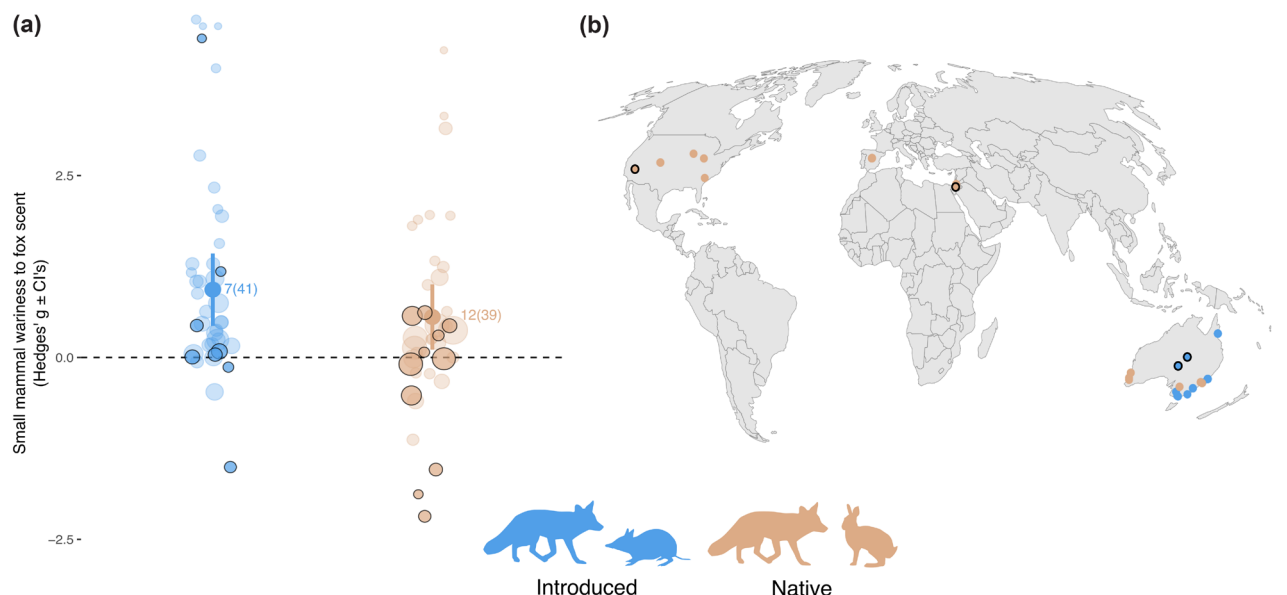
Figure 3. Meta-analysis of experiments assessing the wariness responses of free-ranging small mammals to fox scent. (a) Small mammals respond with similar wariness to the scent of introduced and native foxes. Semi-translucent circles indicate individual experiment effect sizes, the size of which indicates data weight in the analysis (determined by sample size and measure of error). The dark overlaid non-transparent circles with error bars indicate model estimates of overall effect of predator scent on native and introduced wariness responses across studies and their 95% confidence intervals. Numbers indicate the number of studies with the number of experiments in parentheses. (b) Location of the included experiments. Blue indicates introduced fox–prey pairs, beige indicates native fox–prey pairs. There are native fox-prey pairs in Australia comprising of experiments on introduced prey (i.e. red fox and rabbit). Circles with black outlines indicate the results (a) and locations (b) of our field study.

Discussion

The prey naivety hypothesis predicts that animals will respond inappropriately to introduced predators because of a lack of long-term coevolutionary history (Banks and Dickman 2007, Carthey and Banks 2014). Prey should fail to recognise introduced predators or respond ineffectively, inappropriately or excessively compared to prey responding to their native predators (Carthey and Blumstein 2018). We tested the hypothesis with a tri-continental field study – outside and inside the foxes' native range. We found that small mammals responded to fox scent with heightened vigilance regardless of whether the fox is their native or introduced predator. Australian small mammals spent less time at food patches in response to fox scent than Israeli and American small mammals. This result however did not support the proposition that Australian small mammals are hypervigilant or excessively responsive because nut consumption was indistinguishable across regions. Taken together, our field study found that Australian small mammals respond in a similar manner to the foxes' native prey. Placing our results within a meta-analysis further supported the field study, highlighting that predator nativeness does not influence antipredator behaviours, insofar as we can tell.

Rapid environmental change will see the rewiring of global predator–prey networks (Hallam and Harris 2023). Under these rapid ecological shifts prey will face the challenge of adapting to novel predation. Our results suggest that prey can adapt to these challenges by developing new or adapting current antipredator behaviours, should they survive first contact. While the mechanism of antipredator behaviour development will likely be species-dependent, literature exploring the responses of prey to novel predators suggest that rapid development of antipredator behaviours occurs across diverse taxa (Strauss et al. 2006, Wooster et al. 2023a). Available evidence shows that small mammals are savvy even at the earliest years of predator–prey range overlap for which research is available (Wallach et al. 2022). However, it remains likely that prey are vulnerable during initial contact. Conservation attention might benefit prey during this initial period. As efforts to lethally control introduced predators can have unintended ecological effects (Lazenby et al. 2015, Kopf et al. 2017), we suggest that the protection of apex predators (Wallach et al. 2015), habitat (i.e. vegetation cover) or the provision of artificial habitat (Cowan et al. 2020) are more likely to help prey survive novel predation, while promoting the development of crucial antipredator behaviours.

There are four possible limitations to our conclusion that Australian small mammals are not naïve of foxes. Firstly, there is scant information on the responses of threatened (and of course, extinct) small mammals to foxes and other introduced predators. What information is available suggests that threatened species respond as strongly to introduced predators as non-threatened species do (Banks et al. 2018). It is possible that upon fox introduction, native mammals were naive (Luo et al. 2011, Carthey et al. 2017). This lack

of awareness could have driven decline and created predator recognition selective pressures in small mammal populations. Thus, it is likely that species who did not recognise foxes upon introduction went extinct, with fox savvy species remaining. Secondly, the experimental design (responses at food patches to scent) may be unsuitable for detecting whether prey respond ineffectively, inappropriately, excessively, or otherwise, to an actual predation scenario. It remains possible that, in the real world, when faced with live foxes, Australian small mammals are less capable at avoiding deadly encounters than their counterparts who have a longer coevolutionary history with foxes. We can confirm that at least within the limited scenario we studied, we found no maladaptive behavioural differences in the responses of small mammals to the scent of introduced and native foxes, and nor does the literature at large. Thirdly, we did find that Australian small mammals, unlike the foxes' native prey, reduced and increased their time at the food patch in response to the addition of fox scent and herbivore scent respectively. While we are unable to conclude that this behavioural response is in anyway excessive, as it had no discernible effect on foraging, it is possible that local ecological conditions masked a foraging effect. It is also possible, that this result, while statistically significant was a spurious result of the variations expected from an intercontinental field study with a limited number of field sites and species. Finally, the lack of a detectable response in nut consumption at food patches by all small mammals may be an artifact of our choice to conduct our experiments in arid regions. We observed small mammals removing peanuts from the food patches, presumably to consume them in a safer location or to cache for later, consuming other food resources such as vegetation nearby or that had blown into the food patch and even feeding on the experimental herbivore scat. It is possible that lower resource availability promotes caching and opportunistic feeding behaviour, making the experimental design less effective.

Our results suggest that Australian small mammals have rapidly developed antipredator responses to foxes. Rapid evolution and adaptation to introduced species has been documented in a large array of taxa (Strauss et al. 2006). For example, Phillips and Shine (2004) found two snake species (*Pseudechis porphyriacus* and *Dendrelaphis punctulatus*) that have reduced in both gape size and body length since the introduction of the toxic cane toad *Rhinella marina*, preventing them from consuming lethal quantities of poison. The introduction of predators can similarly induce morphological changes in prey (Vermeij 1982), but the most common adaption to the introduction of predators is behavioural (Strauss et al. 2006). The evolution and development of these traits in response to introduction can allow native non-native coexistence, at least in some contexts (Strauss et al. 2006, Wallach et al. 2015).

Predator introduction is widely considered to have driven the decline and extinction of native prey (Doherty et al. 2016). These losses are thought to have been evolutionarily-predetermined, but our work and that of others shows that, insofar as we can tell, prey can develop fully-fledged antipredator responses (Strauss et al. 2006, Banks et al. 2018, Wallach et al. 2022). While prey may retain a level of naivety that has yet to be empirically detected, it is otherwise plausible that declines attributed to introduced predators may instead stem from ecological context, such as the absence of apex predators (Wallach et al. 2010, Wooster et al. 2022) or habitat loss (Fisher et al. 2003, Smith et al. 2019). The ubiquitous recognition of foxes across their native and introduced ranges suggests that prey can adapt to novel predation pressures.

Author contributions

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Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.07031.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.z08kprrkx (Wooster et al. 2023b).

Supporting information

The Supporting information associated with this article is available with the online version.

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