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Outfoxing the fox: Effect of prey odor on fox behavior in a pastoral landscape

Tim A. Andrewartha[1] | **Maldwyn J. Evans[1,2]** | **William G. Batson[3,4,5]** | **Adrian D. Manning[1]** | **Catherine Price[6]** | **Iain J. Gordon[1,7,8,9]** | **Philip S. Barton[1,10]**

[1]Fenner School of Environment and Society, Australian National University, Acton, Australian Capital Territory, Australia

[2]Department of Ecosystem Studies, Graduate School of Agricultural and Life Sciences, University of Tokyo, Tokyo, Japan

[3]Mulligans Flat Woodland Sanctuary, ACT Parks and Conservation Service, Forde, Australian Capital Territory, Australia

[4]Capital Woodlands and Wetlands Conservation Trust, Forde, Australian Capital Territory, Australia

[5]NSW National Parks and Wildlife Service, Blue Mountains Branch, Blackheath, New South Wales, Australia

[6]School of Life and Environmental Sciences, University of Sydney, Sydney, New South Wales, Australia

[7]Division of Tropical Environments & Societies, James Cook University, Townsville, Queensland, Australia

[8]The James Hutton Institute, Cragiebuckler, Aberdeen, Scotland, UK

[9]Land & Water, CSIRO, Townsville, Australia

[10]School of Science, Psychology and Sport, Federation University Australia, University Drive, Mount Helen, Victoria, Australia

Correspondence
Tim A. Andrewartha, Fenner School of Environment & Society, The Australian National University, Building 141, Linnaeus Way, Canberra, ACT 2601, Australia.
Email: tim.andrewartha@anu.edu.au

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Abstract

Invasive mammalian predators have had a devastating effect on native species globally. The European red fox (*Vulpes vulpes*) is one such species where it has been introduced in Australia. A novel but unexplored tactic to reduce the impact of mammalian predators is the use of unrewarded prey odors to undermine the effectiveness of olfactory hunting behavior. To test the viability of unrewarded prey odors in an applied setting we investigated how foxes responded to the odors of three different prey species. We used the odors of two locally extinct native Australian marsupials; the eastern quoll (a smaller carnivore) and eastern bettong (a fungivore), and the European rabbit, an introduced herbivore. Conducting our research over a period of 3 weeks in a pastoral environment in South-eastern Australia, we used video observations of foxes' behaviors, as they encountered the different odors. We found a reduction in the number of fox visits to bettong odors in the third week. In contrast, we observed a sustained number of visits to rabbit odors. Foxes also spent more time investigating rabbit odors and displayed longer durations of vigilance behavior at quoll odors. Our results support the hypothesis that the exposure of wild foxes to unrewarded odors of novel prey species can reduce their interest in these odors, which might translate to a reduction in predation pressure.

Our results also suggest, however, that olfactory pre-exposure may not be as effective at reducing fox interest in a competitor species' odor.

1 | INTRODUCTION

Invasive mammalian predators have been identified as a key threat to biodiversity globally. Thirty invasive mammalian predator species have been implicated in 58% of all bird, mammal, and reptile extinctions worldwide (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016). Prey species most at risk are those with a high evolutionary distinctiveness, and/or that inhabit bounded environments such as islands (Blackburn, Cassey, Duncan, Evans, & Gaston, 2004; Doherty et al., 2016). The impacts of invasive predators on biodiversity occur through a mix of predation (Woinarski, Burbidge, & Harrison, 2015), competition (Glen & Dickman, 2008; Medina, Bonnaud, Vidal, & Nogales, 2014), disease transmission (Medina et al., 2014; Rasambainarivo, Farris, Hertz, & Parker, 2017), and facilitation with other invasive species (Doherty et al., 2016; Doody et al., 2015; O'Loughlin & Green, 2017). Research aimed at understanding the behaviors that underpin these processes may highlight new ways to mitigate the impacts of invasive predators (Greggor et al., 2016).

Invasive predators have a greater impact on populations of native species than native predators do (Salo, Korpimäki, Banks, Nordström, & Dickman, 2007), and a lack of evolutionary experience or "prey naiveté" to invasive predators is regarded as a key factor behind the disproportionate impacts of invasive predators (Cox & Lima, 2006; Sih et al., 2010). Co-evolution between species is a product of both the biotic environment, and the evolutionary potential of the species (Brown & Vincent, 1987). When native species have had limited, or no, previous experience with a similar mode of predation to that employed by the invasive species, the native prey are likely to respond poorly and inefficiently to predation attempts. This can have devastating consequences for small prey populations, potentially leading to their local extinction (Blackburn et al., 2004; Blumstein & Blumstein, 2006; Short, Kinnear, & Robley, 2002). This impact can be exacerbated by significant habitat change and the disruption of species assemblages. The impact of interference, such as the altering of foraging patterns, or the combined impacts of native and invasive predators, can also further increase the pressure on local prey species (Embar, Kotler, Bleicher, & Brown, 2018).

Australia is a continent with unique endemic fauna that have suffered multiple extinction events and range contractions in recent times (Short & Smith, 1994; Woinarski et al., 2015). These extinctions are partially due to the impact of the feral cat (*Felis catus*) (Bengsen, Butler, & Masters, 2011) and European red fox (*Vulpes vulpes*), both invasive predator species (Kinnear, Sumner, & Onus, 2002). Mammals falling within a critical weight range (CWR) of 35–5,500 g have been shown to be particularly vulnerable to predation by these exotic species (Murphy & Davies, 2014). Numerous attempts to reintroduce native species to their previous ranges have failed as a result of predation by the cat and/or fox (Fischer & Lindenmayer, 2000; Moseby et al., 2011; Moseby, Cameron, & Crisp, 2012).

Most current approaches to managing the impact of invasive predator species involve tactics that reduce the size of the local predator population (Saunders, Saunders, Gentle, & Dickman, 2010). Lethal tactics include, shooting, trapping and poison baiting (usually sodium fluoroacetate [1080]) (Saunders et al., 2010), but seldom result in complete eradication (Gentle, Gentle, Saunders, & Dickman, 2007; Thomson, Marlow, Rose, & Kok, 2000). Any reductions in fox numbers are usually temporary, and reinvasion from surrounding areas means efforts must be continuous and across a broad scale to keep numbers low (Gentle et al., 2007; Marlow et al., 2015; Saunders et al., 2010). Poison baiting in buffer zones can reduce the level of reinvasion, however, baiting efforts still need to be maintained (Thomson et al., 2000). The establishment of fenced sanctuaries, using predator-proof fencing can prevent reinvasion, however, the cost of fencing restricts its broad scale use (Moseby & Read, 2006; Parks, Clifton, Best, & Johnson, 2012). Habitat characteristics have also been shown to influence fox predation, with predation rates for reptiles highest in modified landscapes and along habitat edges where shelter is often at reduced levels (Hansen, Sato, Michael, Lindenmayer, & Driscoll, 2019).

To return species to their previous ranges in the presence of introduced predators, new tactics which facilitate some levels of co-existence are needed (Evans et al., 2021; Manning et al., 2021) and approaches that target predator foraging behavior may enhance success. For example, canids, including foxes, detect and locate prey using odor cues (Green et al., 2012; Hansen et al., 2019; Hughes, Price, & Banks, 2010). Olfactory foragers must decide if odors lead to a resource, are indicative of danger or

conflict, or are unhelpful and to be ignored. Experimental studies demonstrate that manipulating prey and predator odor cues can have powerful effects on animal behavior, encouraging the development of new tactics to improve reintroduction success (Price & Banks, 2012; # see references within Jones et al., 2016).

Placing the odor of a locally extinct species in a landscape prior to its reintroduction potentially gives predators an opportunity to repeatedly investigate the novel odor and learn that the odor is unrewarding. This could lead to predators losing interest in the odor because of the costs of investigation, in time and energy, in a process akin to habituation (Price et al., 2020). This concept was tested on wild black rats (*Rattus rattus*) using domestic quail odor (a novel bird species within the environment) and eggs as prey (Price & Banks, 2012). This tactic (Batson, Gordon, Fletcher, & Manning, 2015) targets the beginning of the predation sequence when predators are initially identifying and detecting prey rather than after they have already become motivated to pursue and hunt prey (Endler, 1991). By reducing the likelihood of the predator actively searching for the prey species, this tactic may be effective at reducing predation pressure on species unable to respond effectively to predation, particularly during vulnerable periods such as the initial release phase of a reintroduction. If the prey species is present in the landscape, repeated investigation of unrewarded odor cues may still reduce the value a predator places in the odor due to the increased search cost required to gain a reward. Pre-treating reintroduction sites with prey odor to reduce this predation pressure could allow vulnerable species to re-establish in areas where exotic predators are controlled but still present in low numbers.

Foxes have been shown to modify their behavior in response to odors in three ways. First, they are attracted to the odors of their competitors and predators (Banks, Daly, & Bytheway, 2016). This is thought to help animals gain information about potential resources (i.e., food or den sites). Second, they are wary in the presence of fresh odors from large predators, such as the dingo (*Canis dingo*), which can result in reduced foraging and increased vigilance (Leo, Reading, & Letnic, 2015). However, reported results are from observational studies, and dingo abundance has not been manipulated to test this relationship (Letnic, Ritchie, & Dickman, 2012). Third, foxes also appear to be attracted to novel prey odors (Bytheway, Price, & Banks, 2016). This poses a heightened risk for reintroduced species that present novel odors to foxes. While previous research has observed the response of foxes to other predators and the odors of competitors (Banks et al., 2016; Leo et al., 2015), to our knowledge no studies have looked at the use of odors to reduce fox interest in native species that are at risk of predation.

Here we examined whether wild, free ranging foxes would lose interest in unrewarded odors of novel and familiar prey species as a tactic to assist reintroductions. To achieve this, we quantified the response of foxes to deployed odor cues in a pastoral landscape within the Australian Capital Territory (ACT). We compared the behavioral response of foxes to the odors of a common introduced prey species, the European rabbit (*Oryctolagus cuniculus*), as well as two native Australian species; the near threatened eastern bettong (a fungivore; *B. gaimardi*, henceforth bettong) and endangered eastern quoll (a predator; *Dasyurus viverinus*, henceforth quoll). Both of these native CWR mammals are extinct outside of predator-proof fenced reserves on mainland Australia (Batson et al., 2016; Legge et al., 2018). We asked the following questions.

1. How do foxes respond to the odors of different species? and,
2. Does the behavioral response of foxes towards the odors change over a three-week period?

We monitored the responses of foxes to odors to determine their initial response to the chosen odors, as well as any observed change to the number and duration of visits, and the duration of vigilance behavior. We expected foxes to respond to the novel bettong and quoll odors strongly in the first week of the experiment. By week three, however, we expected foxes would decrease their interest in these unrewarding odors. In contrast, however, we expected their interest in rabbit odors to remain constant throughout the experiment, as this prey species (i.e., reward) was common throughout the landscape.

We discuss our findings in the context of CWR mammal reintroductions in Australia and recommend further research that is needed to develop this novel tactic for improved fox management and species conservation.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted the study at two different pastoral locations that are 6 km apart in the ACT, south-eastern Australia (Figure S1); the National Equestrian Centre (NEC) (Figure S2) and Spring Valley Farm (SVF) (Figure S3). Both study sites are west of Canberra, with the NEC 2 km from the urban fringe (35°20′25″ S, 149°0′26″ E) with the study area covering approximately 2.5 km², and SVF 4 km from the urban fringe (35°16′57″ S, 149°00′19″ E), again with the study area covering approximately 2.5 km².

2.2 | Collection and use of odors

At each location, we installed four or six odor stations, along five different transects. We placed stations along fence lines and in vegetation corridors where foxes are known to move through a landscape (Carter, Luck, & McDonald, 2012; Carter, Luck, & Wilson, 2012). We used bettong, quoll and rabbit odors and compared them to unscented controls. We placed stations a minimum of 200 m apart to increase the independence of observed responses (Cablk, Sagebiel, Heaton, & Valentin, 2008). At each station, we alternated the odors placed each week to reduce the potential for spatial association of a specific odor with a station. At the start of each week, we placed six replicates of each odor within each location to allow foxes to be exposed to multiple sources of the same odor. In each transect we placed at least one of each odor to ensure the spatial availability of the different odors to foxes did not bias the results, approximating a Latin square design. We ran the experiment for 3 weeks because we thought this was sufficient time to elicit a response in the foxes, while balancing logistical constraints related to the field work.

We installed 24 stations at each location. Owing to limited camera availability, only 20 of those stations were monitored with passive infrared (PIR) cameras. Cameras were not rotated between stations. To allow time for the foxes to habituate to the stations, we established them 1 month prior to the recording period. We set up each station with the odor-impregnated material held within a tea strainer, attached to a "lure" stake approximately 0.5 m above the ground, and monitored by a PIR camera (S4 Fig.). We positioned each camera approximately 0.75 m above the ground attached to a camera stake, with each camera stake approximately 5 m from its corresponding lure stake. At each station, we took an image containing a 1 m rule and used this to determine an observation area of a consistent size across all stations. This was done to ensure the camera set up, and vegetation obstructing line of sight did not bias the results.

We collected quoll odors from animals held at Mt Rothwell Biodiversity and Interpretation Centre, bettong odors from animals held at the ANU Research School of Biology Aviaries and rabbit odors from animals held at the Biochemical Radiochemistry Department of Applied Mathematics Research School of Physics Animal Lab at ANU. We used a synthetic coral fleece material as a medium to collect the target species odors. During the preparation of material, we wore latex surgical gloves and minimized direct handling with the use of metal tongs. These precautions were followed in the preparation of material and treatment of material by volunteers. To remove any odor contamination, we placed the tongs

in boiling water prior to use and a different set of tongs were used for the odor of each species of animal. Prior to use we soaked the synthetic fleece material in boiling water and then dried it in direct sunlight to minimize odor contamination. We triple bagged the material in double-seal zip-lock bags and posted it to volunteers with captive populations of the target species for odor collection. Volunteers placed the material in the target animal's sleeping area to collect a "whole body" odor because this is regarded as being more accurate as an indicator of the presence of an individual than urine or feces (Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005). Urine and feces are also used by animals in scent marking for different purposes and may be interpreted differently by the fox (Apfelbach et al., 2005). We chose to use only the whole-body odor to simulate the odor cues of an animal in the environment. After 2 weeks, volunteers collected the material and triple bagged it in double-seal zip-lock bags. The material scented with quoll odor was express posted by volunteers to the Australian National University (ANU) and was frozen at −20°C on arrival to prevent odor degradation (Bytheway, Carthey, & Banks, 2013). The time taken for postage (approx. 24–48 hours) may have led to some degradation of the odor cue of quolls, and the odor cues may have been perceived as "aged" by foxes. Bettong and rabbit odors were collected at the ANU and frozen immediately. We prepared the control material (i.e., no odor) following the same cleaning methods and then froze it at −20°C.

At the start of each week of the experiment, we removed new patches of material for each species from frozen storage. The fresh patches were then placed at the corresponding stations. To reduce any potential cross-contamination from the odors placed in the previous week, tea strainers were thoroughly cleaned using cotton wool soaked in ethanol and allowed to dry before the new odor material patch was placed.

2.3 | Video data collection and analysis

Each recording station had an ltl-5310a Acorn PIR camera set to take 30-second-long video recordings with a 5 s retrigger time and high trigger sensitivity. Where possible, we placed stations in small clearings (approx. 2 m × 4 m) and patches that provided an unobstructed view from the camera to the lure stake to reduce interference from vegetation obstructing vision and movement of vegetation leading to a high number of false triggers. The preference of foxes to the stations surroundings was accounted for by the rotation of odors between stations, as well as the inclusion of station as a random affect in the analysis. We set PIR cameras to record from 6 p.m.

until 9 a.m. the next day as foxes are predominately nocturnal in this environment and to minimize camera triggers from background vegetation during the day. All stations were visited twice weekly to change SD cards and check the equipment was functioning correctly.

Over the duration of the study, we recorded approximately 11,000 video clips. We counted every recording with a fox or multiple foxes as a separate fox visit. Given the preliminary nature of the study, to assess the suitability of the tactic to reduce fox predation, and because identification of individual foxes was not possible (Güthlin, Storch, & Küchenhoff, 2014) we chose not to use a time cut off to distinguish between individual fox visits. If a time cut off between fox visits was used, we risked omitting fox visits. While we have probably counted the same fox as a separate visit, this can be looked at as a potential interaction between a fox and its prey, as opposed to the number of different foxes visiting the odor. Every interaction or encounter between a fox and its prey is possible to lead to a predation event. Data recorded for each visit were time, date, species, number of individuals, if the tea strainer was investigated and if the camera was investigated. We also recorded the duration of visit (time fox spent in view), duration of vigilance behavior displayed, duration of resting while displaying vigilance, the number of vigilance events and scent marking events (Table 1). The classification of behaviors was based upon the ethogram of fox behavior from a previous study (Leo et al., 2015). Once all data were recorded, we grouped vigilance while resting with vigilance behavior due to

TABLE 1 Classification of fox behavior used in this study based on Leo et al. (2015)

Behavior	Classification
Walk (regardless of speed)	Surplus movement
Resting, laying or sitting down	Resting
Remain in area, repeated movements without vigilance	Surplus movement
Sniff tea strainer with head above body level, ears pricked, looking/listening	Vigilance
Remain in area with head above body level, pricked ears, sniffing/looking/listening	Vigilance
Jump	Surplus movement
Laying or sitting down with ears pricked, sniffing/looking listening, raising head	Resting while vigilant
Remain partially in field of view with behavior obscured	Unclassified

the low duration of these behavior categories and similarity in their interpretation.

2.4 | Data analysis

To answer both of our questions, we fitted separate linear (LMM) and generalized linear (GLMM) mixed models for each of our behavior category response variables (fox visitation, duration of visits and duration of vigilance) using the lme4 (Bates, Maechler, Bolker, & Walker, 2015) packages in R (R Core Team, 2021). For question one we fitted models of our response variables against the type of odor factor variable (control [no odor], rabbit, bettong, quoll). For question two, we fitted models of our response variables against the interaction of the odor factor variable and a factor time variable (Week 1, Week 2, and Week 3). We structured the model for question two so that we could account for the effect of time, regardless of treatment and then the nested effects of the treatments compared to the controls within each of the 3 weeks.

$$\text{response} \sim \text{week} + \text{week} : \text{odor} + \text{random effects.}$$

For the fox visitation count data models, we assumed a Poisson error distribution. For the duration of visit and duration of vigilance models we square-root transformed the response variables in order to satisfy the normality. We fitted "odor station" nested within "transect line" nested within "pastoral location" as a random intercept effects to account for the spatial arrangement of our sites and for the repeated measures at each station locality. For the LMM's because not all stations contained visits, we were unable to use the complete nested structure of the design in which case we used individual station code as a random effect. For all models, we examined the histogram of residuals for adequate model fit, and, in the case of the Poisson models, we checked for over dispersion. To plot our results, we used the ggplot2 package (Wickham, 2009) in R. We used R Studio RStudio Team, 2016) as a shell for R.

3 | RESULTS

3.1 | Number of visits

We found a significant negative effect of bettong odor on the number of fox visits in Week 3 (Slope = −2.892, SE = 1.011, p = .004**) indicating that the reduction in

the number of visits was significantly greater at the bettong odors compared to the other odors in the third week of the study. (Figure 2). There was also a downwards trend (not significant) in the effect of bettong odor on the number of fox visits across the 3 weeks. It is worth noting that the number of visits to stations with quoll odor also had a negative trend (not significant) from Week 1 to Week 2 (Table 2) with a negative effect of quoll odor on the number of fox visits seen in Weeks 2 and 3 (Figure 2).

TABLE 2 Table of results showing number of fox visits to each odor, average duration of fox visits to each odor (s) and average duration of vigilance observed by foxes at each odor (s)

	Odor	Week 1	Week 2	Week 3
Visits	Control	13	10	17
	Rabbit	10	24	7
	Bettong	15	5	1
	Quoll	27	3	11
	Total visits	65	42	36
Duration	Control	7.5	3.5	5
	Rabbit	7.1	8.8	9.6
	Bettong	4.1	4	3
	Quoll	11.1	7	8.5
Vigilance	Control	0	0.5	0.1
	Rabbit	0.4	0.7	0.9
	Bettong	0.6	0.4	1
	Quoll	4.6	0.7	2.3

3.2 | Duration of visits

There were no significant differences in the total number of visits foxes made to the different odors during the study (Figure 1).

The average duration of fox visits at all odors, except for rabbit odor, was greatest in Week 1 (Table 2). Foxes spent a significantly longer total duration of time at stations with rabbit odor compared to the other odors and unscented controls during the study (Rabbit Slope = 0.627, SE = 0.275, R^2 = 0.068, p = .024) (Figure 1).

Foxes spent significantly more time investigating rabbit odors compared to the other odors in Week 2 of the study (Rabbit, Slope = 1.420, SE = 0.557, p = .015*) (Figure 2).

3.3 | Duration of vigilance behavior

Foxes spent significantly more time engaged in vigilance behavior at quoll odor (Slope = 0.814, SE = 0.232, R^2 = 0.098, p = .001***) compared to the rabbit (Slope = 0.236, SE = 0.224, R^2 = 0.098, p = .295) and bettong (Slope = 0.124, SE = 0.283) odors as well as unscented controls. This duration of vigilance behavior was observed over the 3 weeks of the study (Figure 1).

Foxes spent significantly more time engaged in vigilance behavior at quoll odor compared to the other odors during Week 1 of the study. While there were no other significant effects, the length of fox vigilance behavior at quoll odor appeared to reduce during Week 2, and subsequently increase in Week 3 (Figure 2).
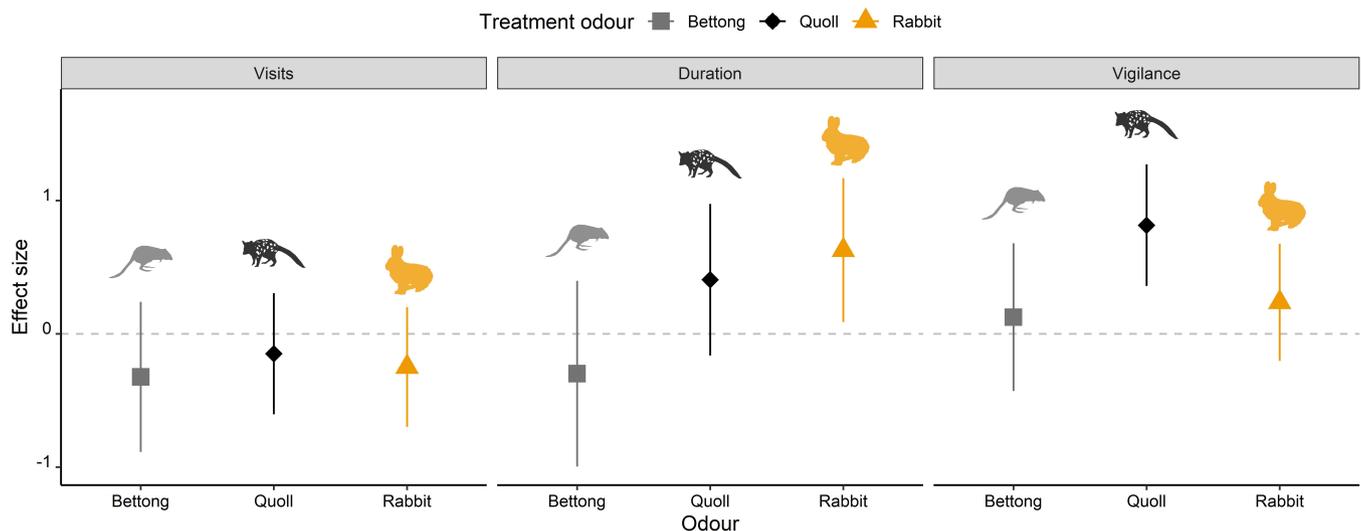

FIGURE 1 Effects (model coefficients) of odor treatment on the number of visits (R^2 = 0.004), duration of visits (R^2 = 0.068) and duration of vigilance behavior (R^2 = 0.098) by foxes, comparing odor sites to control sites. Error bars represent 95% confidence intervals
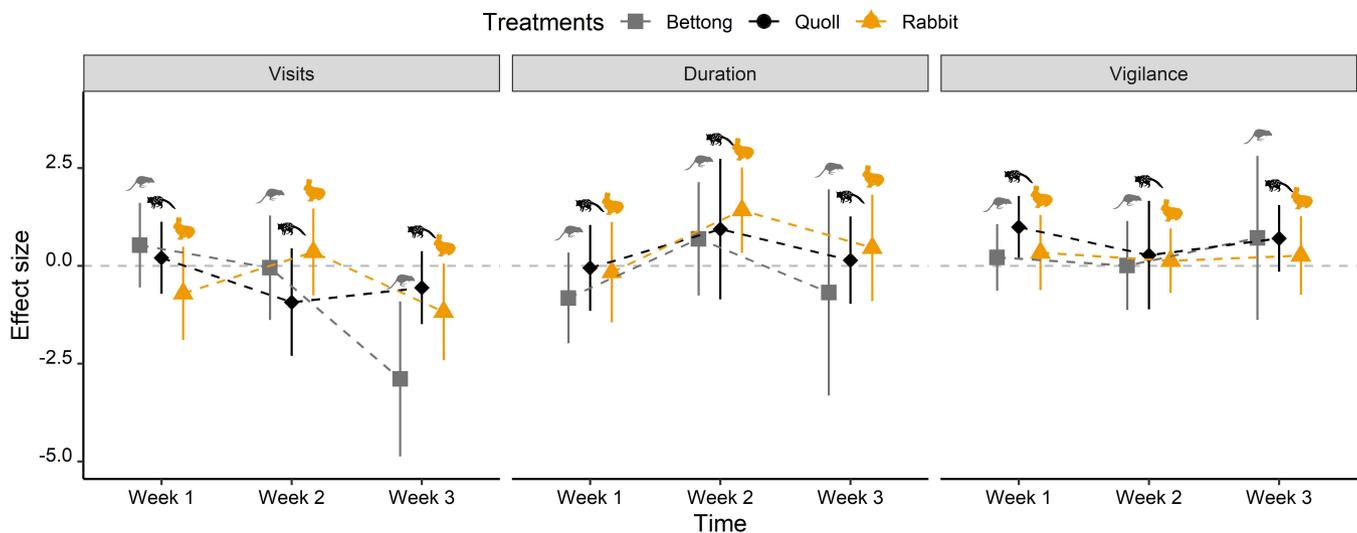
FIGURE 2 Effects (model coefficients) of the interaction between odor treatment and week on the number of visits ($R^2 = 0.015$), duration of visits ($R^2 = 0.092$) and duration of vigilance behavior ($R^2 = 0.095$) by foxes, comparing odor sites to control sites. Error bars represent 95% confidence intervals

4 | DISCUSSION

We have shown that free ranging wild foxes lost interest in a locally extinct novel prey species (bettong) odor over time. However, foxes initially responded with higher levels of vigilance towards the odors of a novel smaller carnivore and maintained the level of vigilance over the 3 weeks. While a negative trend was observed in the number of fox visits to the quoll odor, a three-week pre-exposure did not lead to a greater reduction in interest than was observed to all odors, including unscented controls. The higher levels of vigilance observed at quoll odor suggest that foxes can recognize this species odors as belonging to a carnivore (Leo et al., 2015). The maintained response of vigilance observed towards carnivore odor may be explained by the level of risk or threat perceived by the fox from a competitor, and the severity of the potential consequences. This would particularly be the case if the fox was unable to recognize the odors as belonging to the quoll but was able to recognize a general carnivore odor (i.e., it cannot tell whether the odor means a threat or prey). The information gained from carnivore odors about potential competitors, likelihood of predation and resource distribution may also account for the maintained interest despite a pre-exposure of odors.

Our results suggest that a pre-exposure of foxes to the odor of a locally extinct prey species could help to reduce the impact of foxes on the species immediately after translocation/reintroduction. This finding is important because it provides a complementary approach to fox management beyond the traditional approach of lethal removal of foxes from the landscape. It may also be applied to other

olfactory-led predator species, with recent experimental evidence demonstrating the effectiveness of an olfactory pre-exposure to protect shorebird populations from a range of olfactory mammalian predators in New Zealand (Latham et al., 2019; Norbury et al., 2021; Price et al., 2020). By conditioning the fox to ignore the odors of a prey species, this tactic targets the predator behavior at the point of prey detection, before an encounter occurs (Endler, 1991; Price & Banks, 2012). As a result, the naivety of prey species to the predator, and their ability to escape, should not prevent this tactic from being effective. While this will not eliminate the detection of prey by other means such as visual and audible cues, it may reduce the likelihood of encounters for a period of time.

4.1 | How do foxes respond to the odors of different species in a landscape?

Our results show foxes investigated an unfamiliar prey species odor (bettong), and a known prey species odor (rabbit) at the same rate (visits), however, they spent a longer duration investigating the odors of a known prey species in the landscape (rabbit). There were no significant differences between the number of visits, and durations of vigilance behavior observed by foxes at rabbit and bettong odor. The duration of fox visits, however, was significantly higher at rabbit odors as compared to all other odors. While novel odors have been identified as attractive to foxes, rabbits are a common prey species of foxes at the two sites, and so dedicating more time to the investigation of their odor would likely have led to a

reward via predation prior to, and during, the study. This would explain the equal number of visits observed, but greater dedication of time by foxes to a known-rewarded odor compared to the two novel no reward odors. In contrast, quoll odor was of significantly greater concern to foxes than bettong and rabbit odors with a raised duration of vigilance observed. The vigilance response to quoll odor could suggest that foxes have perceived the odor as indicative of a potential competitor or higher order predator. The vigilance may have indicated the engagement of anti-predator responses in preparation for conflict with a competitor or predator, or alternatively it may have indicated the investigation of a weaker competitor's odor in order to engage in interference competition (Banks et al., 2016; Clark et al., 2005; Leo et al., 2015; Pamperin, Follmann, & Petersen, 2006). Quolls are a smaller species than the fox, but both species use similar resources (Commonwealth of Australia, 2010; Godsell, 1983), however, foxes are also known to directly depredate on quolls (Wilson et al., 2020). If local foxes associated quoll odors with a competitor, the observed increased duration of vigilance would be expected (Leo et al., 2015). This response might also be expected to the odors of a higher order predator such as a dingo (Banks et al., 2016). Alternatively, this heightened level of fox interest in a quoll odor could be a result of its novelty (Bytheway et al., 2016). If the latter was the case, however, we would expect to observe raised levels of vigilance at the bettong odor, and would expect foxes to lose interest in it over the 3 weeks.

4.2 | Is there a change in the response of foxes to the odors over time?

Over the 3 weeks of the study the total number of fox visits was seen to decline with a significant negative effect observed in Week 2 and 3, relative to Week 1 (Figure 2). The effect of time on the total number of fox visits can be seen in the simpler model of total fox visits by week, however, the reduction in the number of visits was not equal for all odors. Over the period of 3 weeks, fox interest in bettong odors declined as indicated by the reduction in the number of visits. This decrease was not observed for rabbit odors (Figure 1). In contrast to rabbits, eastern bettongs are locally extinct and have been extinct on mainland Australia for approximately 100 years (Short, 1998). Consequently, bettong odor was a novel odor to local foxes and there had been no reward reinforcement prior to, or during the experiment. The reinforcement of the investigation of an olfactory stimulus via a food reward has been demonstrated experimentally in male Long-Evans rats (*Rattus norvegicus*)

(Devore, Lee, & Linster, 2013). When presented with a pair of odors, reinforcement of one via reward led to a preference for the rewarded odor, and subsequent faster acquisition by rats of resources marked with the rewarded odor.

We are trying to exploit a similar, but opposite foraging tactic in the fox, whereby an odor not associated with a reward will be ignored. If a fox is confronted with a bettong odor, the lack of any food reward may lead to foxes choosing to ignore the odor. The differential loss of interest observed to bettong odor, in contrast to rabbit odors, supports the proposition that the reduced interest was due to the pre-exposure of odors and not just natural variation. The period of a three-week pre-exposure of bettong odor tested in this study was sufficient to reduce the number of fox visits to the odor from 15 in the first week of the study, to one in the third week of the study. While this suggests a pre-exposure of odors for 3 weeks will lead to a significant reduction in the number of investigations of the odor by foxes, it may still be insufficient to facilitate the reintroduction, and post release survival of bettongs in the presence of foxes, in part due to the vulnerability of the species to fox predation. Further, the impact of availability of other food resources, time of year, or other local conditions requires investigation to determine the effectiveness of the tactic, and whether it can be broadly applied.

The duration of visits to any odors did not decrease across the 3 weeks, however, investigations to rabbit odors were significantly longer in Week 2. The longer investigations of rabbit odor in Week 2 that were also observed at non-significant levels in Week 3 may not have been present in Week 1 because of the introduced novel odors in the landscape. It is possible that foxes reduced their investigation of rabbit odors to dedicate time towards the investigation of novel odors; however, further testing would be required to confirm this hypothesis.

The level of vigilance shown by foxes to quoll odor was significantly higher in the first week of the experiment but was sustained at non-significant levels across the 3 weeks of the experiment. Further, while an initial decrease in vigilance at quoll odor from Week 1 to Week 2 was observed, it was seen to rise again in Week 3. This result may explain why quolls appear particularly susceptible to fox predation when they escape outside predator proof fences (Wilson et al., 2020). There was, however, a downwards trend in the number of fox visits to quoll odor from Week 1 to Week 2. It is possible that a longer exposure of quoll odor may lead to reductions in the number of fox visits, and a reduction in the duration of vigilance observed; however, this would have to be tested in an experiment of a longer duration.

5 | CONCLUSIONS

Presently, fox management is targeted at the removal and exclusion of foxes from specific areas and does not address the impact of the remaining foxes that evade control or reinvade after control. While fox management can be effective for reducing the many impacts of foxes on the pre-existing biodiversity and pastoral/ agricultural industries (Saunders et al., 2010), it is often not to a level sufficient to allow the reintroduction of native species (Hayward et al., 2012; Moseby et al., 2011; Moseby et al., 2012). Our study has demonstrated a proof-of-concept for the use of a pre-exposure of odors to reduce predation of newly reintroduced species that were locally extant. However, it remains unclear how effective this potential tactic might be in practice as it is not known how the target predator species would remain uninterested in the odors of reintroduced prey once these prey are available.

Previous reintroduction projects have attempted to establish species in the presence of foxes and found that even with the application of various tactics, such as anti-predator training to avoid foxes, fox predation was a significant barrier to success (Moseby et al., 2012). The tactic of a pre-exposure of foxes to odors, is not suggested to be used in isolation, but alongside other fox control methods. The pre-exposure tactic addresses the specific issues of the reintroduction of a species in the presence of an olfactory-reliant predator that would otherwise likely target vulnerable reintroduced individuals. Using the tactic could provide these founder individuals with a period of relaxed predation pressure in which they could become established in a new environment.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All data used for this study are being made publicly available through the ANU Data Commons and a link will be provided as soon as it is available.

ETHICS STATEMENT

All applicable institutional and/or national guidelines were followed for the care and use of animals. The work was completed under ANU animal ethics protocol number A2016/26.

ORCID

Tim A. Andrewartha https://orcid.org/0000-0002-1840-9213
Maldwyn J. Evans https://orcid.org/0000-0001-7025-2287
Adrian D. Manning https://orcid.org/0000-0003-0989-9203
Iain J. Gordon https://orcid.org/0000-0001-9704-0946

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