Behavioural responses of free-ranging western grey kangaroos (*Macropus fuliginosus*) to olfactory cues of historical and recently introduced predators

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Abstract

Predation risk influences foraging decisions and time allocation of prey species, and may result in habitat shifts from potentially dangerous to safer areas. We examined a wild population of western grey kangaroos (*Macropus fuliginosus*) to test the efficacy of predator faecal odour in influencing time allocated to different behaviours and inducing changes in habitat use. Kangaroos were exposed to fresh faeces of a historical predator, the dingo (*Canis lupus dingo*), a recently introduced predator, the red fox (*Vulpes vulpes*), a herbivore (horse, *Equus caballus*) and an unscented control simultaneously. Kangaroos did not increase vigilance in predator-scented areas. However, they investigated odour sources by approaching and sniffing; more time was spent investigating fox odour than control odours. Kangaroos then exhibited a clear anti-predator response to predator odours, modifying their space use by rapidly escaping, then avoiding fox and dingo odour sources. Our results demonstrate that wild western grey kangaroos show behavioural responses to predator faeces, investigating then avoiding these olfactory cues of potential predation risk, rather than increasing general vigilance. This study contributes to our understanding of the impact of introduced mammalian predators on marsupial prey and demonstrates that a native Australian marsupial can recognise and respond to the odour of potential predators, including one that has been recently introduced.

Key-words: behavioural responses, western grey kangaroos, predator odour, historical/introduced predators, predation risk

Introduction

Predation risk strongly influences the behaviour of prey (Lima & Dill, 1990) and under perceived threat of predation, prey may become more vigilant (e.g. Blumstein et al., 2003; Laundré et al., 2001; Lingle & Wilson, 2001) and/or modify their use of space, shifting from risky to safe areas to prevent an encounter with a potential predator (Lima, 1998). Predator odours often elicit anti-predator responses in prey, similar to those observed in situations of high predation risk (see Apfelbach et al., 2005), as predator-derived odours may be perceived by prey species as cues to increased risk of predation. Predator odours suppressed feeding by white-tailed deer (*Odocoileus virginianus*; Swihart et al., 1991), significantly reduced abundance and activity of northern pocket gophers (*Thomomys talpoides*; Sullivan et al., 1988), reduced spatial movement of meadow voles (*Microtus pennsylvanicus*; Perrot-Sinal et al., 1999) and increased vigilance of red bellied tamarins (*Sanguinus labiatus*; Caine & Weldon, 1989). Therefore, predator odours have the potential to influence the activity pattern and distribution of prey species.

Prey species generally respond more strongly to the odour of predators that they have coevolved with (Apfelbach et al., 2005). Therefore Australian prey may be more responsive to the odours of historical predators, as insufficient time has elapsed to evolve recognition of the odour of recently introduced predators. Australia's unique mammalian fauna evolved in biogeographical isolation for around 35 million years. The recent introduction of exotic predators has caused naïve prey to face evolutionary unfamiliar predators, and as a consequence, many small native Australian mammals have experienced significant declines in distribution and abundance (Burbidge & McKenzie 1989). However, not all native prey have declined; rapid evolutionary responses to predation should be expected in prey that are impacted strongly by a new predator and which also have a large enough population and genetic variation to allow for an evolved response (Strauss et al. 2006). There is some evidence suggesting that some small Australian species may have evolved rapid anti-predator adaptations to cope with the new predators (Anson & Dickman 2013; Kovacs et al. 2012). We examine here antipredator responses to historical and recent predators of a large macropod marsupial, the western grey kangaroo (*Macropus fuliginosus*).

Macropod marsupials have a well-developed olfactory system (Salamon, 1996) and use olfactory cues to avoid potentially toxic food (Jones et al., 2003). Only a few studies have explored how macropods detect and respond to olfactory cues of predation. Tammar wallabies (*Macropus eugenii*) increased alertness when exposed to predator odours in a laboratory experiment (Mella et al., 2010a), and captive western grey kangaroos reduced feeding activity in response to dingo (*Canis lupus dingo*) odours (Parsons et al., 2007; Parsons & Blumstein, 2010). However, captivity and predator-naïvety may influence anti-predator behaviour (Blumstein et al., 2002; Miller et al., 1990); therefore studies on predator odour recognition should be extended to wild prey populations. Field experiments on the responses to potential predator odours of free-ranging prey can complement results obtained in captive studies and help to clarify and validate the role and behavioural consequences of olfactory cues of predation (Mappes et al., 1998; Wolff, 2003).

We exposed a free-ranging population of western grey kangaroos to predator (dingo and fox, *Vulpes vulpes*) and herbivore (horse, *Equus caballus*) faeces to determine if they could (1) discriminate between faeces derived from different species and (2) perceive faecal odour as a cue of predation risk, altering their behaviour and/or habitat use. We hypothesised that predator faecal odours would provoke an increase in vigilance and a change in the kangaroos' space use. Since prey responses to olfactory cues of predation can depend upon the co-evolutionary relationship between prey and predator (Müller-Schwarze, 1972), western grey kangaroos were expected to respond most strongly to dingo cues than to fox cues. Dingoes are a major predator of kangaroos (Whitehouse 1977; Shepherd, 1981; Thomson, 1992) and they share an evolutionary history in Australia of over 3000 years (Corbett, 2008). Foxes have imposed a much shorter historical predation pressure on kangaroos (< 200 years); nevertheless they are known to influence kangaroo behaviour (Coulson, 2008; Banks et al., 2000).

Methods

Study site

The study took place at Whiteman Park Recreation and Conservation Reserve, Perth, Western Australia (31° 49' S; 115° 56' E). Foxes have been regularly recorded in the park for over 25 years, but dingoes are absent (Bancroft, 2005; Corbett, 2008; Hyder and Dell, 2009). Five minute observations of focal animals (focal sampling, continuous recording) were recorded from a hidden position with a Sony HDR-CX6EK Handycam, from a distance of at least 50 metres at four different locations within the reserve. We chose locations over 2 km apart, in an attempt to avoid monitoring the same individuals and thus pseudoreplication, since all kangaroos were free ranging and not individually marked. All locations were open homogeneous, grassy areas surrounded by trees and shrubs. Observations at each location consisted of a pre-test phase and a test phase, carried out on consecutive days with similar weather conditions (no rain or heavy wind), as both temperature (Merril, 1991) and wind affect vigilance behaviour (Hayes &

Huntly, 2005), habitat choice (Yasue et al., 2003) and perceived predation risk (Hilton et al., 1999). Kangaroos were filmed at dusk for two hours, when grazing is their main activity (Short, 1986). Gender (male, female, unknown), age group (pouch young, juvenile at foot and adult) and distance to the focal animal's nearest neighbour were estimated by eye with binoculars at the beginning of each focal sample.

Study design

Pre-test phase

The first part of the study consisted of recording kangaroo activity at the different study locations (i.e. the same locations where the tests were then carried out) to determine occurrence of basic behaviours and average time allocated to feeding, vigilance, locomotion, grooming and social interactions. This controlled for any location-specific behaviour, and provided a baseline to test the unscented control against, ensuring that the effect of the experimental odours did not extend to the other odour areas.

Test phase

In the second part of the experiment each location was virtually divided into four 25 m^2 plots, one containing the odour of a historical predator (dingo), one the odour of a recently introduced predator (fox), one a herbivore odour (horse) and one an unscented control. Plots were separated by a buffer of 20 m to ensure independence of the plots. Responses of western grey kangaroos to predator odours decrease with distance and are no longer significant at 12 m (Parsons et al. 2007). Scent sources were placed on white ceramic tiles; all four treatments were presented simultaneously and were randomly assigned to the plots. Within each plot the odour was presented on three tiles (2 m apart) placed diagonally across the 25 m^2 region (Fig.1). Tiles were placed in the plots just before dusk, prior to the arrival of the kangaroos at the locations. Five minute individual focal recordings were made for randomly selected kangaroos within the odour plots, with a range of 6-14 individual kangaroos filmed in each plot. We are confident that no kangaroo was filmed in more than one plot on any night.

Odour sources

Predator odours were fresh faeces obtained daily from dingoes and foxes maintained in captivity on a meat diet at Caversham Wildlife Park, Perth, Western Australia. We used horse faeces donated by private owners as a non-predator control odour. Faeces were placed on the tiles within a few hours of collection. A single bowel motion was used for each tile to resemble odour concentration encountered by kangaroos under natural conditions. In the unscented control plot, tiles were placed in the same pattern to control for visual interference but with no odour treatment. All tiles would presumably retain some human scent, but this would be the same for all odour treatments. Care was taken to avoid any cross-contamination between odours; faeces were placed on the tiles at dusk directly from their containers using new gloves for each sample and tiles were used only once.

Data Analysis

Behavioural analysis

JWatcher Video Version 1.0 (www.jwatcher.ucla.edu) was used to record the time (seconds) each focal kangaroo was engaged in various behaviours during both phases of the study (Blumstein & Daniel, 2007). Foraging was scored as kangaroos standing pentapedally with their head down biting or chewing food. Vigilance was scored as kangaroos standing on hind legs with head and ears raised, or standing pentapedally with head up scanning the surroundings. Self grooming (e.g. pouch cleaning and scratching) and interaction with other individuals (aggressive and affiliative) occurred in short bouts and were combined as ‘other behaviours’. Locomotion while searching for food included kangaroos walking pentapedally with head down. Approaching (hopping towards the tiles), investigating (sniffing the tiles), avoiding (pentapedally walking away from the tiles), fright response (jumping abruptly) and flight response (fast hopping away from the tiles) were all scored as separate behaviours. Time spent out of view during the 5 min focal sample filming (i.e. after vacating the 25 m^2 experimental region) was also recorded as a category.

Statistical analysis

As the times engaged in activities were compositional (summed to 5 min), they were transformed as ln(x+1) of the ratio of time spent engaged in each activity to that spent foraging (as foraging was the most commonly observed activity), after Aitchison (2003). As different behaviours were recorded for each individual kangaroo, behaviours for an individual kangaroo could not be considered independent; therefore we used a multivariate repeated measures (RMANOVA) design that makes no assumptions about the covariance matrix of the test (Rencher, 2002). RMANOVA of the transformed data was used to establish if location or odour influenced the time allocated to different behaviours. If a significant RMANOVA was identified, Student Newman-Keuls (SNK) *post hoc* tests for univariate ANOVAs were necessary to determine the nature of the response (i.e. specific behavioural responses to pair-wise comparisons of odours).

The before phase data were compared for the four locations to ensure there were no site-specific differences in kangaroo behaviour, with location as a between subjects factor and the transformed behaviour times of each kangaroo as the repeated measure. As there was no influence of location, data from the four locations were pooled. Any influence of the experimental procedure for testing odours on non-scented controls was tested by comparing the pre-test phase with the no-scent treatments, with pre or test phase as the factor and the transformed behaviour times of each kangaroo as the repeated measure. To examine the effect of various odours, we used the treatments (i.e. dingo, fox, horse and no scent) as between subjects factors and the transformed data for behaviour allocation of each kangaroo as the repeated measure. Since gender (Jarman, 1987; Pays & Jarman, 2008), age (Heathcote, 1987) and distance from the nearest neighbour (Coulson, 1999) may influence kangaroo behaviour, the effects of these variables were included in separate RMANOVA analyses as covariates. Dummy variables for categorical covariates were calculated after Draper and Smith (1998) and Cohen (2008), with two dichotomous variables used to code for three groups (i.e. 0,1 for males, 1,0 for females and 1,1 for unknown).

For the behaviours fright (jumping abruptly) and flight (escaping by fast hopping away from the tiles) the frequency of occurrence data were analysed using a Log-Likelihood Goodness of Fit analysis for the test phase, as these behaviours occurred so quickly it was unlikely that any differences in time engaged in these activities could be found (i.e. differences from 0 sec were small due to the short duration of these rapid responses). Statistical analyses were completed using StatistiXL Version 1.7 (Nedlands, Western Australia) and IBM SPSS Statistics V20 (Armonk, New York). Values are presented as mean ± standard error unless stated otherwise.

Results

A total of 109 western grey kangaroos (50 females, 44 males and 15 unknown) were recorded during the study, 51 in the pre-test phase and 58 in the test phase. There were 78 adults, 27 juveniles and four joeys. There was no significant influence of location on kangaroo behaviour during the pre-test phase ($F_{3,47} = 0.212$, $P = 0.888$), so data from the four locations were subsequently combined. There was also no difference in kangaroo behaviour between the pre-test phase and the unscented control plots ($F_{1,57} = 0.327$, $P = 0.570$).

During the test phase, foraging and locomotion while searching for food were the main activities observed (Table 1), with highly significant differences in the time kangaroos spent engaged in various behaviours relative to foraging ($F_{8,47} = 8.34$, $P < 0.001$). There was an overall significant effect of odour on time spent engaged in various behaviours ($F_{3,54} = 2.88$, $P = 0.044$) relative to foraging. Time spent engaged in locomotion while searching for food (SNK $P \geq 0.319$), vigilance (SNK $P \geq 0.210$) and ‘other’ behaviours (SNK $P \geq 0.244$) relative to foraging were not influenced by odour. However, kangaroos spent more time approaching and investigating tiles with fox odour than those with horse (SNK $P = 0.008$ and $P = 0.013$ respectively) and no odour (SNK $P = 0.022$ and $P = 0.032$ respectively). Kangaroos spent more time avoiding the tiles with fox odour compared to those with dingo (SNK $P = 0.007$), horse (SNK $P = 0.002$) and no odour (SNK $P = 0.013$). Kangaroos vacated areas (moving toward vegetation cover) and remained out of view for longer in plots treated with dingo odour compared to areas with horse odour (SNK $P = 0.040$).

The covariates age ($F_{1,52} \leq 2.68$, $P \geq 0.108$), gender ($F_{11,52} \leq 0.970$, $P \geq 0.329$) and distance to nearest neighbour ($F_{1,53} = 0.001$, $P = 0.972$) did not influence the allocations of time to the different behaviours. There were also no significant interactions of these factors with the various behaviours ($F_{8,45} \leq 0.480$, $P \geq 0.864$; $F_{8,24} \leq 1.60$, $P \geq 0.152$; $F_{8,24} = 0.615$, $P = 0.760$ respectively).

A fright response (abrupt jump; Appendix 1) was observed 10 times for kangaroos investigating predator odours (7 dingo, 3 fox) and 4 for non-predator odours (3 for horse and 1 for no odour), but there was no significant log-likelihood difference between observed and expected responses ($G_3 = 5.35$, $P = 0.148$). However, there was a significant difference between observed and expected frequencies of flight responses for the different odours ($G_3 = 8.54$, $P = 0.038$), with kangaroos fleeing more often from predator odours (6 dingo; 4 fox) than control odours (3 horse; 0 no odour).

Discussion

We found that western grey kangaroos did not increase vigilance relative to foraging in the presence of predator faecal odours, but there was a strong effect of predator faeces on behaviour. Fright and flight responses and a subsequent change in space-use were observed in predator-scented plots, with kangaroos avoiding (fox) or vacating the area (dingo) after close investigation of the predator odours. Although faeces may not represent a cue for imminent threat of predation (Banks et al., 2003), they can increase perceived predation risk (Jonsson et al., 2000), as they may indicate the presence of a predator in the area. In this study, predator faecal odour was clearly perceived as a strong cue of potential predation threat, and kangaroos modified their space-use, rather than increasing their general vigilance.

Western grey kangaroos closely investigated all odours presented, approaching and sniffing the scented plots. This response was presumably odour driven, as kangaroos did not approach or investigate unscented (control) tiles. Other prey species closely investigate olfactory cues to acquire information about odours. These include sheep (*Ovis aries*; Pfister et al., 1990), red-necked pademelons (*Thylogale thetis*; Blumstein et al., 2002; Ramp et al., 2005), black-tailed deer (*Odocoileus hemionus columbianus*; Sullivan et al. 1985) and yellow-bellied marmots (*Marmota flaviventris*; Blumstein et al., 2008). Parsons & Blumstein (2010) observed inspection of predator odours by captive western grey kangaroos. This behaviour appears necessary to assess the risk of predation before an appropriate behavioural response is initiated (Fishman, 1999; Sih, 1992). Interestingly kangaroos spent more time investigating (approaching and sniffing) fox odour than the control odours, which may indicate greater interest in assessing fox cues, likely because they may be encountered frequently at the study site (Jackson et al., 2007), or because more time or information is required to interpret the level of potential predation threat indicated by fox faeces.

We interpret the fright and flight response to predator odours, and the subsequent avoidance of the odour sources, as fear of increased predation risk to both predators. Similar avoidance of predator odours has been observed in many studies (see Kats & Dill, 1998) and fleeing after investigation of predator urine and faeces has been observed in captive western grey kangaroos (Parsons et al., 2007; Parsons & Blumstein, 2010).

It has been suggested that macropods may respond to the cues associated with predator odours in a generic way and not specifically to certain species of predator (Blumstein et al., 2002). Predators related at the family level, such as dingoes and foxes, share common compounds in their odours, which can be recognised by the prey (Nolte et al., 1994; Fey et al., 2010), and presumably have similar odoriferous chemicals in their faeces (Stoddart, 1980; Dickman & Doncaster, 1984). However, macropods also have experience-based predator recognition (McLean et al., 2000; Blumstein et al., 2002), and since foxes occur at the study site and dingoes do not (Bancroft, 2005; Jackson et al., 2007), the western grey kangaroos may have experienced the predation risk posed by foxes and responded accordingly. Indeed, anti- predator responses tend to be greater if the subject has previous experience of the predator (see Apfelbach et al., 2005), and kangaroos did appear to show more interest in fox odour. Responses to dingo odour were likely retained even if this predator is not currently present in the study area because of the long historical period of co-evolution kangaroos and dingoes have shared. Dingoes were widespread on the Swan Coastal Plain at the time of European settlement, but are now considered regionally extinct (Corbett, 2008; Hyder and Dell, 2009).

Our study of western grey kangaroos does not support the hypothesis that many Australian marsupials are unable to identify cues of introduced predators such as foxes (Dickman and Doncaster, 1984; Dickman, 1992). It is apparent that marcropod marsupials demonstrate anti-predator responses when encountering cues of introduced predators (this study, Mella et al., 2010a; Parsons et al., 2007), and could clearly distinguish between predatory and non-predator species. Responses to both foxes and dingoes indicate that a long period of co-history is not a prerequisite for detection of a potential predator. These findings for western grey kangaroos and other macropods (Mella et al. 2010a) are in contrast to the responses of smaller marsupials which appear not to modify their behaviour to avoid the odour of potential predators (Russell and Banks, 2005, 2007; Mella et al., 2010b; but see Anson & Dickman 2013; Kovacs et al. 2012), although native Australian rodents may do so (Russell and Banks, 2005, 2007;

but see Banks, 1998; Banks et al., 2003). The effects of predation risk vary with a number of factors, including body mass (McNamara and Houston, 1987). It would be of interest to examine differences in predator recognition and anti-predator responses in a broader allometric and phylogenetic context to better understand patterns in anti-predator behaviour and its implications for conservation.

Our results demonstrate that wild western grey kangaroos are wary of predator faecal odours and tend to escape and be deterred from these cues, suggesting that they associate fox and dingo-scented areas with predation risk. Western grey kangaroos responded to olfactory cues of predation from both historical and recently introduced predators, although close investigation seemed necessary for odour recognition. Avoidance rather than vigilance was the predominant anti-predator response for free-ranging kangaroos facing potential predation risk. This study has obvious management and conservation implications and is relevant to understanding the patterns and evolution of mammalian predator odour recognition.

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Table 1: Ratio (mean time in seconds) of various behaviours to foraging, for western grey kangaroos in response to predator and control odours. Values are mean ± S.E. (n = number of kangaroos observed). There were no differences in behaviour between the pre-test phase and control odour. During the test phase, for behaviours where a significant effect of odour was identified, different superscripts indicate significant differences.

	Pre-test (n = 51)	Test (n = 58)			
Behaviour		control (n = 8)	horse (n = 25)	dingo (n = 16)	fox (n = 9)
food searching	1.39 ± 0.114	1.47 ± 0.166	1.34 ± 0.166	2.22 ± 0.792	0.86 ± 0.409
vigilance	0.97 ± 0.080	1.35 ± 0.225	1.68 ± 0.271	2.63 ± 0.820	2.64 ± 1.128
other	0.36 ± 0.071	0.58 ± 0.174	0.46 ± 0.180	0.67 ± 0.318	0.02 ± 0.014
approaching	0.00 ± 0.000	0.00 ± 0.000^{a}	0.64 ± 0.309^{a}	1.91 ± 0.843^{ab}	3.90 ± 1.512^{b}
investigating	0.00 ± 0.001	0.07 ± 0.070^{a}	0.64 ± 0.298^{a}	1.62 ± 0.794^{ab}	3.51 ± 1.36^{b}
avoidance	0.00 ± 0.000	0.00 ± 0.000^{a}	0.35 ± 0.162^{a}	0.88 ± 0.463^{a}	3.57 ± 1.750^{b}
fright	0.00 ± 0.001	0.00 ± 0.004	0.28 ± 0.272	1.42 ± 0.739	0.853 ± 0.839
flight	0.00 ± 0.000	0.00 ± 0.000	0.52 ± 0.503	1.78 ± 1.833	2.86 ± 1.833
out of view	0.48 ± 0.089	0.04 ± 0.036^{ab}	0.18 ± 0.080^{a}	1.60 ± 0.788^{b}	1.70 ± 1.100^{ab}

Figure legends

Figure 1: Schematic diagram of the experimental design of the test phase of the study. All the odours were presented simultaneously and each was randomly assigned to a region.