Predator scent induces differing responses in two sympatric macropodids

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Abstract

When prey species encounter the scent of a predator they must make a decision on how to respond. This may be either to ignore, flee, hide or alarm call. While many species are able to derive detailed information from the chemical cues associated with predator scent, for some the decision to respond is often made without being able to identify the actual location and intentions of the predator. Depending on the sociality and ecology of the species, it may pay to flee or to engage in predator inspection where knowledge is impure. We tested for this in two sympatric marsupial macropodids, the parma wallaby (*Macropus parma*) and the red-necked pademelon (*Thylogale thetis*), as little is known of how these species detect and respond to olfactory cues of predation risk. We observed that when presented with a synthetic predator scent mimicking dog urine, the social forager, *T. thetis*, tended to spend more time in close proximity of the predator odour, while the solitary forager, *M. parma*, exhibited an aversive response. The results suggest that social and ecological constraints on the sensory modalities used in predator detection may influence how macropodids respond to olfactory predator cues.

Running Title: Responses to predator scent in macropodids.

Introduction

Assessing the risk of predation is typically achieved with imperfect knowledge (Abrams 1994) and yet the assessment of threat is critical to an animal's survival. If an animal overestimates the threat and flees, it incurs a decline in fitness as costs are commonly not negligible. If it underestimates the threat, it may be killed. Much effort has gone into modelling the switch from knowledge to actual decision-making as prey respond to predator presence (e.g. Lima and Bednekoff 1999; Lima and Dill 1990; Sih 1994; Sih and McCarthy 2002). Pivotal in developing these models is the removal of the assumption of prey immediately fleeing predators upon detection, as not every predator a prey encounters represents a direct threat (Ydenberg and Dill 1986). As such it is beneficial for prey to assess the risk of capture once the presence of a predator has been detected, utilising whatever sensory cues they have at their disposal.

Prey species exhibit a variety of behavioural responses to the threat of predation, such as increased vigilance, social grouping and avoidance strategies. These responses rely on sensory cues to evaluate the risk of predation and enable prey to reduce the risk by responding appropriately. Assuming some level of imperfection of knowledge, prey animals are confronted by uncertainty when determining what the 'optimal' response should be. Prey species typically flee when the risk of capture and/or uncertainty reaches a given threshold (Brown 1999). This threshold is dependent upon the fitness and hunger status of each animal, their metabolic rates, their relative difference in speed to the predator and the distance to refuge. It is also dependent upon the ability of the prey species to identify accurately the predator's intentions as they vary temporally (Lima and Bednekoff 1999). Prey may reduce the level of uncertainty by undertaking predator inspection, but must weigh-up the additional costs and benefits of employing this strategy (Dugatkin and Godin 1992; Fishman 1999). By engaging in predator inspection, prey may inadvertently increase the risk of capture by increasing the likelihood of an encounter with a predator. Contrasting with this is the potential reduction in risk as prey can obtain important information on the predator's intentions (Lima and Dill 1990).

All extant species in the Family Macropodidae, which includes wallabies, kangaroos and tree-kangaroos, have been subjected to predation from both past and present land-based and aerial predators (Jarman and Coulson 1989). As such anti-predator behaviour should be firmly established in the behavioural repertoires of all macropodid species, although documented evidence of anti-predator behaviour is limited to a handful of studies. Group size, a common predator detection and avoidance strategy (Elgar 1989; Lima 1995; Pulliam 1973; Roberts 1996), has been positively linked to anti-predator behaviour in a number of macropodid species (see Blumstein *et al.* 2003), ranging from small wallaby species (e.g. *Macropus eugenii*, Blumstein *et al.* 1999) to large kangaroo species (e.g. *Macropus giganteus*, Coulson 1999). They exhibit a wide variety of vigilance behaviour, whether solitary or social, and almost universally engage in foot-thumping as an alarm signal when threatened (e.g. Blumstein *et al.* 2000). Small species typically engage in cryptic behaviour to avoid detection and are mostly solitary, particularly those inhabiting dense vegetation habitats (e.g. le Mar 2002), although this does not hold as a steadfast rule. Some small species seek shelter in dense undergrowth but forage in open areas, typically engaging in grouping behaviour when they do (e.g. *Thylogale thetis*, Wahungu *et al.* 2001).

There may be life history and ecological reasons why some prey species may not necessarily use, or be able to use, visual, aural and olfactory cues equally when assessing predation risk (see Peacor 2003). The environment in which prey abide is important, as the ‘many eyes’ strategy can reduce the amount of time allocated to vigilance in open environments (e.g. Boland 2003; Cresswell 1994), however environmental impediments such as thick understorey may limit the effectiveness of this strategy. Spatial limitations on the collective detection of predators are an important constraint influencing the anti-predator strategies adopted by prey (Lima and Zollner 1996). Within this mix of confounding factors, strong selection pressure should be exerted for prey utilising as many sensory cues as possible in order to improve their knowledge of their immediate predation risk, and hence reduce the level of uncertainty in their threat of capture.

Use of olfaction as a predator cue has been shown to last considerable periods of isolation from predators in other mammal species such as Orkney voles (*Microtus arvalis*) (Calder and Gorman 1991). Prey species relying on scent to evaluate predation risk where visual cues are not often available has previously been explored (e.g. Abrams 1994; Bouskila *et al.* 1995; Jedrzejewski and Jedrzejewski 1990; Kats and Dill 1998), but as yet this question has had little experimental testing with macropodids (but see Blumstein *et al.* 2002b).

We test this assumption by comparing the behavioural responses of two similar-sized and sympatric species in the Macropodidae. While the chosen species respond to the same canid predator, their foraging modes, social systems and use of space should influence the sensory cues they would typically rely upon to assess predation risk. We hypothesised that the differing behavioural ecology and anti-predator strategies of the two species (see methods) would manifest in their reactions to the presence of an olfactory predator cue, although we caution that any conclusion about these being adaptations is limited as we only compare two species (see Garland and Adolph 1994). We tested individuals that have been reared in captivity for ease of observation. Captivity is often observed to weaken behavioural responses however our aim was not to quantify the magnitude of response but to make inferences from response direction.

Methods

Study species

The study was conducted at Cowan Field Station, approximately 45-km north of Sydney, Australia, and adjacent to Muogamarra Nature Reserve (33°37′35″ S, 151°09′20″ E). Experimental trials were conducted on the parma wallaby (*Macropus parma*) and the red-necked pademelon (*Thylogale thetis*), both of which are predated upon by feral dogs (*Canis lupus*), the dingo (*Canis lupus dingo*) and the red fox (*Vulpes vulpes*) (Newsome *et al.* 1997). These wallabies are considered to be in the critical-weight range (i.e. particularly susceptible to predation), with *M. parma* (average weights of males 5.0 kg, females 4.0 kg) slightly smaller on average than *T. thetis* (average weights of males 7.0 kg, females 3.8 kg) (Strahan 2002). *Macropus parma* lives along the ranges of eastern New South Wales, primarily inhabiting wet sclerophyll forest and occasionally dry sclerophyll forest with thick understorey (Maynes 1977). It is a solitary species, foraging among small open patches that are connected by runways allowing passage through the thick understorey (Maynes 1977; Read and Fox 1991). These herbivores are nocturnal, with peaks in activity around dawn (Ord *et al.* 1999). They utilise acoustic and olfactory signals for social communication and courtship (Ord *et al.* 1999), so given the reliance on dense vegetation for cover, it is reasonable to assume that *M. parma* would rely heavily on acoustic and olfactory cues to detect predators.

By comparison, *T. thetis*, which is also present along the eastern ranges of NSW, is an edge specialist. It is essentially crepuscular, utilising rainforest and dry sclerophyll forest during the day while moving short distances out into open clearings to forage at night (Johnson 1977). Most individuals spend more than 80 % of their time within 15 m of the forest edge (Wahungu *et al.* 2001). Johnson (1980) attributed their night use of open clearings as evidence of a trade-off between foraging and predation risk, and identified heightened levels of vigilant behaviour when in the open. When foraging in open clearings *T. thetis* aggregate in small groups, with group size increasing with distance from cover (Wahungu *et al.* 2001). In the field *T. thetis* exhibit the typical response of most macropodid species, decreasing the amount of time allocated to vigilance behaviour with increasing group size (Wahungu *et al.* 2001). This contrasts with captive trials that have found no effect of group size on vigilance in *T. thetis* (Blumstein *et al.* 2002a). *Thylogale thetis* consume a diet of grass, herbs, shrubs and vines (Wahungu *et al.* 1999). Wahungu (2001) postulated that in open areas *T. thetis* rely upon visual and sound cues for the detection of predators.

Experimental design

The behavioural responses of these two species to predator odour were assessed by conducting a series of captive trials. These captive-reared individuals have never come into direct contact with a predator although they may have possibly heard or smelt them in the adjacent reserve. One subject was tested at a time, with three males and three females of each species used. A three-pen enclosure was used; each pen was 5 by 6 m constructed of 2-m high chain-mesh fencing, with 60 % Sarlon green shade-cloth attached to the fence to minimise external distractions. Subjects were free to move among pens via an open door in each of the end pens that linked them to the central transitional pen. The daily food requirements of each animal in the form of kangaroo pellets was halved and distributed equally between the two end pens so that foraging was encouraged in both pens. A pile of straw was placed on a discrete synthetic fibre sheet at the furthest end of the pen approximately 2-m adjacent to the food. Both the food and straw were changed daily. Water was freely available in the transitional pen which also encouraged movement among pens.

A single subject was released into the transitional pen so as not to bias choice of the two end pens, with the subject then free to move among pens. Each trial was run for a total of four days. At the beginning of day three the straw from one pen was sprayed with approximately 100 ml of Plant Plus, a synthetic predator odour manufactured by Roe Koh & Associates Pty Ltd. The choice of pen for spraying was alternated between consecutive subjects. Plant Plus is a foliar application typically used for the protection of seedlings from browsing damage caused by mammals (Roe Koh & Associates Pty Ltd 2000). We were interested in its ability to stimulate a fear response in the animal, releasing odours analogous to those produced by predators such as dogs through their urine although the active constituents are currently protected by Roe Koh & Associates Pty Ltd. The product was developed after the testing of a variety of products and finding that dog urine had strong repellent response in the swamp wallaby (*Wallabia bicolor*) (Montague *et al.* 1990). Captive and field trials of Plant Plus have resulted in significant prevention of browsing damage in the European rabbit (*Oryctolagus cuniculus*), the brushtail possum (*Trichosurus vulpecula*), the brown hare (*Lepus capensis*) and *W. bicolor* (Morgan and Woolhouse 1998; Roe Koh & Associates Pty Ltd 2000). This study represents the first instance of using this product to elicit behavioural responses in animals purely on the basis of olfaction, rather than including any potential taste aversion as the exact mechanism of function has yet to be documented.

Movements of the subjects within the pen system were monitored using overhead video cameras and recorded using the computer program EthoVision 2.3 (Noldus Information Technology 2001). Infra-red sensitive video cameras (Sony HAD CCD image sensor) with a variable focal-length automatic iris lens were positioned at a height of 5-m above each pen. Red-filtered lights fitted to the side of each pen were used to provide lighting at night. Video footage of the pens was recorded using a time-lapse VCR (Panasonic AG-6040), with the tapes changed over daily when the animals were fed each morning. Nightly patterns of movement were monitored between dusk and dawn.

Data analysis

We measured the response of the subjects to Plant Plus by comparing the amount of time spent in each of the pens and comparing time spent in close proximity to the food in each of the end pens before and after treatment. Time spent in the pens after the application of

Plant Plus was compared using the non-parametric Mann-Whitney U test and Monte Carlo significance estimates (using 95 % confidence levels and 10,000 randomisations) and carried out in SPSS v 12.0.1 (SPSS Inc., 2003). Subjects were judged to be in close proximity of the feeding station, which was adjacent to the straw with or without the odour applied, when they were recorded as being within 2 m. The frequency of such visits and the percentage time spent at a feeding station per 30 minute time block were averaged for each species and the values compared between treatments for each species using the Mann-Whitney U test and Monte Carlo significance estimates.

It should be noted that the aim of this study was to identify trends in response of the two species, and not experimentally quantify the magnitude of response (effect size). As experiments were conducted in captivity the latter would necessitate cautious assessment when comparing to responses exhibited in more natural settings. Comparing tests performed as one-tailed, as opposed to two-tailed, would therefore be appropriate, rendering P values significant at the 0.05 level when $\alpha = 0.10$ (Quinn and Keough 2002). P-values reported are two-tailed unless otherwise stated.

Results

For *M. parma*, subjects spent significantly more time in the pen without odour after the Plant Plus treatment was applied ($n = 12$, $z = -2.714$, $p = 0.006$), with a similar significant decrease in time spent in the pen with the odour ($n = 12$, $z = -2.829$, $p = 0.004$, Figure 1). No change in the use of the transitional pen was observed ($n = 12$, $z = -1.155$, $p = 0.263$). These trends were consistent among individuals, although one subject exhibited no obvious response to the treatment. Aversion to the odour was confirmed by observations such as individuals pausing in the doorway of the odour pen followed by retreating to the control pen.

In contrast, despite the trend for *T. thetis* subjects to spend more time in the pen with the odour applied this result was not significant (*n* = 12, *z* = -1.559, $p_{(two\text{-}tailed)}$ = 0.126, $p_{(one\text{-}tailed)}$ = 0.062). Individuals of *T. thetis* were observed to approach the treated straw and engage in sniffing and heightened vigilance behaviour. A significant decrease in the use of the pen without the odour was observed when the test was considered one-tailed (*n* = 12, *z* = -1.790, $p_{(two\text{-}tailed)}$ = 0.077, $p_{(one\text{-}tailed)}$ = 0.039). Like *M. parma*, no change in the use of the transitional pen was observed (*n* = 12, z = -1.501, $p_{(two\text{-}tailed)}$ = 0.141, $p_{(one\text{-}tailed)}$ = 0.071). Looking at a finer scale, the frequency of visits and the percentage of time spent by *M. parma* within 2 m of the feeding stations, which were directly adjacent to the straw, were not different for either pen after treatment (Table 1). The frequency of visits by *T. thetis* to the feeding stations in the two pens increased marginally in the odour pen and declined marginally in the no odour pen although these trends were not significant. The percentage of time spent within 2 m of the feeding stations followed a similar trend but variation among individuals was considerable.

Discussion

We conducted captive trials on two sympatric macropodids that support the hypothesis that behavioural responses to olfactory predator cues may be dependent upon the prey's foraging mode, social system, and use of habitat and other sensory cues. At the level of the pen, patterns of either avoidance in *M. parma* or attraction in *T. thetis* were evident. These shifts in the amount of time spent in the pens after the application of the predator odour, Plant Plus, were up to 30 to 40 percent for some individuals. We suggest that although tests were not significant at the 0.05 level for *T. thetis*, the results give good cause to believe that responses were biologically important. We justify this by noting that the measures recorded were indirect and that different individuals typically exhibit significant amounts of variation in responses. Given large treatment effects by some individuals it would be remiss to disregard these results on the basis of an arbitrary significance level (see Robinson and Wainer 2002). Behavioural responses were backed up by observational evidence, with *M. parma* exhibiting strong aversive responses including fleeing upon scent detection and *T. thetis* actively engaging in sniffing and increased vigilance in close proximity to the Plant Plus, possibly attempting to engage in predator inspection (see Fishman 1999).

It is likely that macropodids respond to the olfactory cues associated with predator urine in a generic fashion and not specifically to predators the animals have had direct experience with (Blumstein *et al.* 2002b), although species-specific responses have been shown in other systems (see Jedrzejewski and Jedrzejewski 1990). This lends credence to the responses of both macropodids tested here to a generic synthetic urine product, yet it does not imply that the behavioural responses engaged in post-detection should be similar. No previous research has examined the response of *M. parma* to predator urine, however Blumstein *et al.* (2002b) ran captive trials investigating predator recognition by *T. thetis* to carnivore and herbivore faeces and urine. They observed that while not significant, *T. thetis* spent an average of 13 % more time foraging in close proximity to dog urine than an unfamiliar herbivore urine. They suggest that the ability of these individuals to respond to predator urine has been lost in only a generation or two of captivity. In contrast to this, in our study we tested similarly maintained individuals and yet observed attraction to predator odour, conforming to the weak trends found by Blumstein *et al.* (2002b). By allowing for predator inspection as a deliberate anti-predatory strategy we find that these individuals still retain the ability to respond to predator scent.

Laundré *et al.* (2001) described a ‘landscape of fear’, in which prey individuals live in a environment where predation risk varies spatially and temporally (see Sih and McCarthy 2002). It is probable that for some species the scent of predators may be always present, although of varying intensity. How different species and even individuals decipher this information to provide some indication of the level of risk of predation they may face is an important ecological question. At the core of this paradigm is the relationship between the detection of predator odour and subsequent assessment of predation risk; an essential component of many species' anti-predator strategies. Chemosensory perception enables prey species to identify the past presence of a predator, typically through urine and faeces but also from social markings (Kats and Dill 1998). But this relationship is not straightforward, as Banks *et al.* (2000) suggested that prey species have little respite from predation risk when odorous waste-deposits accumulate in the environment. This works both ways, with odour from both prey and predator species effectively 'giving each other away'. While many species have been documented as deriving detailed information from predator scent, it remains unclear as to how much information macropodids gain, particularly in a sometimes saturated environment.

Sociality has been linked to differences in home range size and habitat use in macropodids (Jarman and Coulson 1989; Kaufmann 1974). Studies examining sympatric macropodids have confirmed that the more social the forager, the greater the extent of space use (e.g. Evans 1996). Given the interaction between space use and sociality in the adoption anti-predator strategies, there is a strong biological basis that sensory cues used in assessing predation risk will also vary along this scale. The solitary species that inhabits typically closed forest, *M. parma*, spent less time in areas with predator odour. The social forager that utilises open clearings, *T. thetis*, chose to inspect the odour more closely and did not flee.

Our findings indicate that both *M. parma* and *T. thetis* were able to detect predator scent and respond in a way that can be explained by current anti-predatory theory, despite being captive-reared animals and predator-naïve, although more evaluation of the behavioural responses is warranted and we would caution about inferences of adaptation made on two-species studies. Despite this we suggest that space use and sociality may be inextricably linked when determining the behavioural responses of macropodids to predator scent. It would be pertinent to continue to explore olfactory communication in more species of macropodid and replicate trials with field experiments. In light of current exploration of the use of predator scents to deter macropodids from causing browsing damage and from spending time on road-side verges (and subsequently becoming roadkill), our results suggest that the use of predator scent as a repellent may be species specific.

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Tables

Table 1

Comparison of frequency of visits and the percentage of time spent within 2 m of the feed stations in the no odour and odour pens before and after the application of Plant Plus. Mann-Whitney U tests were used to compare means and p-values are reported for both one and two-tailed tests.

Species	Response	Pen	Before Mean ± SE	After Mean ± SE	z	$p_{(two\text{-}tailed)}$	$p_{(one\text{-}tailed)}$
Macropus parma	Frequency	No Odour	5.98 ± 1.29	9.51 ± 2.04	-1.121	0.309	0.154
		Odour	6.66 ± 1.52	8.62 ± 1.28	-1.121	0.309	0.154
	Within 2 m	No Odour	17.29 ± 4.66	21.86 ± 5.85	-0.801	0.486	0.244
		Odour	19.77 ± 6.75	18.84 ± 8.28	-0.480	0.702	0.350
Thylogale thetis	Frequency	No Odour	10.39 ± 3.07	4.92 ± 1.57	-1.441	0.180	0.091
		Odour	13.66 ± 5.13	17.68 ± 7.55	-0.480	0.702	0.352
	Within 2 m	No Odour	18.69 ± 4.81	15.32 ± 7.85	-1.281	0.240	0.121
		Odour	18.05 ± 3.33	25.21 ± 6.38	-0.961	0.394	0.195

Figure Legends

Figure 1

Change in mean percent duration (± 95 % confidence limits) spent by *Macropus parma* and *Thylogale thetis* subjects in each of the three pens after treatment. Control values were subtracted from treatment values to provide the treatment change. Significance at the 0.05 level is indicated by an asterisk while significance in the no odour pen for *T. thetis* is for the one-tailed test.

Figures

Figure 1