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Feeling Vulnerable? Indirect Risk Cues Differently Influence How Two Marsupials Respond to Novel Dingo Urine

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Abstract

In Tasmania, introduced predators are becoming more common. How Tasmanian prey respond to novel predator cues is of particular interest for their survival and management. Prey response to predator scents may depend on whether predator and prey share an evolutionary history and may be influenced by indirect risk cues such as perceived shelter or safety in the environment. To simultaneously explore the effects of indirect and direct risk cues (predator scent) on free-living Tasmanian pademelons (*Thylogale billardierii)* and brush tail possums (*Trichosurus vulpecula*), we placed dingo (*Canis lupus dingo*) urine scents inside and outside a 25 -m^2 selective feeding enclosure to mimic a heterogeneous risk landscape. Despite the lack of a historical relationship between dingoes and Tasmanian fauna, pademelons and possums demonstrated flight and vigilance when confronted with the novel scent outside the enclosure. According to our index of deterrence, number of successful entries/approaches, both species were deterred. However, responses *inside* the safe enclosure differed according to species. For instance, pademelons made more approaches/entries into the enclosure and fled more following approaches to scent marks both inside and outside the enclosure. In comparison, possums only exhibited similar responses outside the enclosure, and there was no effect of stimulus inside the safe compound. Our findings suggest that small animals may be pre-adapted to avoid some predators they have not previously been in contact with, and that brush tail possums are more likely to respond to predation cues when exposed and vulnerable. Ultimately, the cumulative effects of direct and indirect risk cues may either increase or reduce a repellent response.

Introduction

Predators may communicate silently through olfactory compounds in urine, faeces, and glandular secretions. Infochemicals and metabolites consist of both non-polar (short-chain fatty acids and their metabolites) and polar (sulphur-based and associated carrier proteins) compounds that interact to provide multiple layers of information to conspecifics (Brennan 2009). Information within urine can communicate territorial markers (Gorman & Trowbridge 1989; Brennan 2009), oestrous (Sankar & Archunan 2008), nutritional status (how recently a predator has fed; Gelperin 2008), and a time-stamp of the predator’s void (Wyatt 2003) Degradation of these molecules over time will reduce the level of information available in the chemical compound (Wyatt 2003).

Prey, however, should intercept and decipher infochemicals, if doing so enhances survival. Such heterospecific eavesdropping (Schoeppner & Relyea 2009) is poorly understood. Despite an extensive literature on intraspecific information contained in predator scents (Müller-Schwarze 2006; Brennan 2009; Sankar & Archunan 2008; Gelperin 2008), it is unclear what degree of information can be extracted from predator compounds by prey. Some prey may avoid predator scents simply because strong scents alter the palatability of nearby foods (Kimball & Nolte 2006), although other species can detect and investigate even a single molecule of predator-produced scent (Brennan 2009). A number of aquatic (Fraker 2009) and terrestrial (Pillay et al. 2003) species can even discriminate between wastes from predators that have, or have not, fed on conspecifics.

A better understanding of prey responses to predator cues may help lead to the development of humane deterrents where animals encroach on human habitats, as well as be used to enhance conservation successes. For instance, predator scents may be used to teach predator naive or orphaned animals to be wary of potential predators (Griffin et al. 2000). This approach is particularly important in Australia where critical weight range animals (35–5500 g) on the mainland have been decimated by the introduction of predators (Chisholm & Taylor 2009), possibly more so than any where else in the world (Salo et al. 2007). Small extant native species such as eastern barred bandicoots (*Perameles gunnii*) and Tasmanian bettongs (*Bettongia gaimardi*) have limited contact with mammalian predator cues, potentially making them more vulnerable to threat from newly introduced predators such as the European fox (*Vulpes vulpes*). Conversely, with the subsequent decline of primary predators, some native species have become overabundant (Letnic et al. 2009). For instance, brush tail possums (*Trichosurus vulpecula*) and Tasmanian pademelons (*Thylogale billardierii)* are considered primary pests to the forestry industry (McArthur et al. 2000), and there is great interest for non-invasive tools to assist conservation and management of native fauna.

Historical Predators and Body Size

Some prey have the ability to discriminate between the urines of historic and novel predators, and primarily respond to historically relevant ones (Jedrzejewski et al. 1993; Barreto & MacDonald 1999). For instance, Domestic cattle (*Bos taurus*), which evolved with wolves in Eurasia, can distinguish among predator cues from wolves and the novel mountain lion (Kluever et al. 2009). Similarly, western grey kangaroos (*Macropus fuliginosus*) can discriminate among canine urines from the novel coyote (*Canis latrans*) and sympatric dingo (*Canis lupus dingo*; Parsons et al. 2007; Parsons & Blumstein 2010). The ability of potential prey to distinguish among scents secreted from different predator species is consistent with the olfactory acuity of mammals (Gelparin 2008; Brennan 2009). Though, this ability might seem more adaptive for large than small mammals, because it would not be efficient for large prey to avoid foraging in an area where small or insignificant predators had been detected. Small prey, on the other hand, should generally avoid foraging in an area where *any* predator has been detected. A *leitmotif*, or general, response (Stoddart 1980) is observed when small prey respond to the scents of novel predators (Woolhouse & Morgan 1995; Rosell & Czech 2000).

Among Tasmanian species, Mcevoy et al. (2008) demonstrated that (despite their small size) Tasmanian swamp rats (*Rattus lutreolus velutinus*) respond to scent from the predatory sympatric spotted-tail quoll (*Dasyurus maculatus*), but not from the introduced fox (*Vulpes vulpes*). The lack of response to foxes is interesting because swamp rats are small mammals and should respond to a wide range of predator scents and also because canids (e.g. feral dogs) have inhabited Tasmania since 1803. Dingoes have been present on the mainland for 5000 yr (Wilton et al. 1999) but have never been present in Tasmania.

Indirect Risk Cues

Shelter or perceived safety may affect prey responses to potential danger (Lima & Dill 1990). Indirect risk cues such as distance from protective cover, 'escape-ability' (While & McArthur 2005; Liley & Creel 2008), and the amount of vegetative cover (Searle et al. 2008) may reduce predation risk and therefore influence prey response. Surprisingly, some prey may be more responsive to indirect cues, such as moonlight and cloud cover, than to direct predator cues (Orrock & Danielson 2004; Preisser et al. 2007). For instance, oldfield mice (*Peromyscus polionotus*) respond to indirect cues of predation (exposed food trays outside of cover) more prominently than predator scents (Orrock et al. 2004). Vegetation cover was more likely to predict vole (*Microtus spp.*) foraging space than scent-based predator cues (Pusenius & Ostfeld 2002). These findings are not anomalies. In a meta-analysis, Verdolin (2006) found that habitat characteristics had stronger effects than either predator odour or live predators. Sometimes, direct and indirect cues work additively, but not in the absence of one another. Neither recorded owl calls nor the full moon (which exposes prey to visually hunting predators) had any effect on the behaviour of white-footed mice (*Peromyscus leucopus*) when treatments were introduced separately. However, when owl recordings were combined during a full moon, prey reduced seed foraging by nearly 70% (Schmidt 2006). Similarly, the cumulative effects of indirect and direct danger cues may enhance the strength and area of effect (Orrock & Danielson 2009).

We investigated whether urine from the novel dingo would elicit aversive behavioural responses from two potential allopatric prey, Tasmanian pademelons (*Thylogale billiardierri*) and brush tail possums (*Trichosurus vulpecula*). In a recent review (Apfelbach et al. 2005), few studies included a component of indirect fear cues or prey vulnerability. Thus, we mimicked a heterogenous risk landscape by including scent marks both inside and outside a sheltered feeding enclosure. We asked the following questions. First, does dingo urine cause either pademelons or brush tail possums to avoid entering a feeder placed inside a fenced enclosure? Second, does it cause animals to flee the feeder once inside? Third, does it influence the number of approaches to enter the enclosure? Fourth, does urine outside the protective compound induce animals to take flight outside the compound?

Materials and Methods

Site Description

Trials were carried out in a 0.5 -ha lot in Maydena, Tasmania (42°45′21S, 146°37′26E) 87 km west of Hobart in southwestern Tasmania. Although many small Tasmanian mammals are rare, brush tail possums and pademelons are locally abundant and considered pests to both agriculture and forest industries (McArthur et al. 2000). Maydena is particularly overgrazed by pademelons and possums. The Department of Primary Industries and Water (DPIW) selected this site for longitudinal studies because of the high population density of both species in the vicinity and because it is located on cleared land immediately surrounded by preferred plantations (*Pinus radiata*) and native wet sclerophyll forests (John Dawson, DPIW, pers. comm.). Potential mammalian predators of both species include spotted-tail quolls (*Dasyurus maculatus),* Eastern quolls *(Dasyurus viverrinus)*, and Tasmanian devils (*Sarcophilus harrisii*).

A 25 -m^2 selective feeding enclosure was composed of 75 × 50 × 2 mm weldmesh walls held in position by picket star posts and ground pegs (Fig. 1). Browsers gained entry and exited the compound via one-way entry/exit doors. The feeder, consisting of an automatic food dispenser attached to a 44 gallon drum, was used to dispense abundant and attractive food (rolled oats soaked in an 18% alcoholic turbo yeast solution with added salt and sugar) for an extended period.

Animal Density and Identification

Local animal density was established prior to trials and resulted in the selection of this research site by the DPIW as part of the ‘Alternatives to 1080 Programme’ (http://www.daff.gov.au/forestry/national/cfa/1080). Animal visitation was quantified by counting the number of animals that entered the compound each night. During a 6 -mo period where animals acclimated to the enclosure, 60–70 different pademelons and 30–40 different brush tail possums

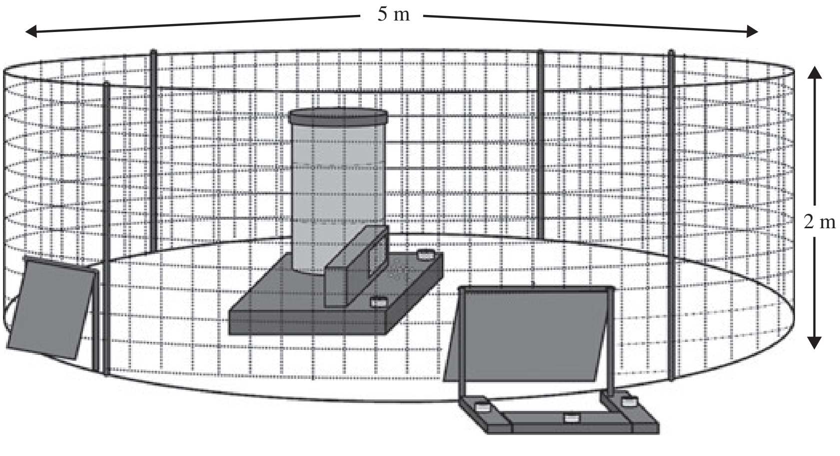

Fig. 1: Enclosure compound in Maydena, Tasmania. The 25 -m^2 compound was constructed of 75 × 50 × 2 mm weldmesh walls held in position by picket star posts and ground pegs. Food placed in a single 44 gallon drum was used to attract animals for recruitment into experimental trials.

Table 1: Visitations of 5 possums with bleach-marked patterns (above) and 5 pademelons (below). Three of the pademelons did not participate in the experiment

Period	Before					Treatment			After				
Day	1	2	3	4	5	1	2	3	1	2	3	4	5
Possum													
19:00		C			E				E	D	E	C	
20:00	A								E	E			*D*
21:00													
22:00	B	C	D			C	C,A		E	C,D	C	C,A	*A*
23:00	C		A		A	C	C				C,A	E	
0:00		C,D,E	A,E										
1:00								C	A	E		C	*E*
2:00	A			C,E				C					*C*
3:00	C						C				E		
4:00									A	E	E		
5:00						E	E						
6:00													
Pademelon													
9:00		G			G	G							*G*
20:00													
21:00													
22:00					G						G	G	
23:00													
0:00		F		B			G	G					
1:00			F							G			
2:00	F										G		
3:00													
4:00		F											
5:00													
6:00													

were captured on the property and released, some of which were marked with bleach patterns for future identification (Ivo Edwards, pers. comm.). Animals that entered the compound often fed to satiety and left after extended feeds. Prior to trials, ten of these individuals (five of each species) were marked with unique bleach patterns. Among these animals, no individuals visited the trial area every day; however, on days when individuals visited, they tended to enter the area twice daily (Table 1). No animal visited the feeder more than three times in 1 d. The trial period corresponded with the autumn breeding period of both species; however, trials were observational only and animals chose whether to participate or decline interaction with the predator signal.

Trials

Experiments were conducted on free-living pademelons and brush tail possums between 27 Mar. and 17 Apr. 2008. Pure-bred dingo urine was collected 17 Feb. 2008 from the Australian Dingo Conservation Association in Michelago, NSW. We limited our collection to pure-bred dingoes, because domestic dog scent differs in pH, turbidity, and Gas Chromatograph profiles (Ken Dods pers. comm., Chemistry Centre WA) as well as eliciting different behavioural responses from marsupials (Blumstein et al. 2002; Parsons unpublished data). All dingoes were fed chicken carcasses prior to collection. We avoided freezing samples because of the possibility of denaturing carrier proteins (Schultz et al. 2000). Urine was collected and stored fresh (refrigerated under minimal head-space) as active constituents vary with time since void (Müller-Schwarze 2006; Ken Dods, pers. comm., Chemistry Centre WA) and because we have observed aged (>12 wk) dingo urine to have no aversive effect on western grey kangaroos (unpublished data) – despite its strong smell to our noses.

Five evenings (26, 27, 29, 31 Mar.; 4 Apr.) were selected as the 'before period' to quantify all activity in the observational area. Each treatment consisted of three 40 ml Petri dishes of dingo urine (a typical void) placed at the entry of the compound and two further dishes placed at the feeding trough (Fig. 1). During the treatment period (5–8 Apr.), we placed the dingo urine out nightly at 18:00 h and recorded video for 6–12 h each night.

Following the treatment period, we allowed one week before quantifying behaviour during an 'after' period with no dingo urine (12–17 Apr.). We chose not to employ scents from non-predatory species as further control. While this design is often utilized in the literature (Apfelbach et al. 2005), we are not aware of any published studies where scents from herbivores or omnivores generate fear-based responses from other animals – despite the presumed potential for neophobic responses. All trials were illuminated with two long-distance infra-red lights (Raymax 200 series lights) and recorded onto a Panamax NV VZ1 video camera with night vision capability.

Analysis

Our trials were observational only and did not involve manipulation of animals. Therefore, because we could not confidently identify most animals, we accepted that some counts would be repeated among individuals. That said, we know that multiple animals participated because we concurrently saw a mix of marked and unmarked animals. To eliminate the effects of re-sampling individuals within a day, we calculated hourly averages and then used one value per day (of the average of the averages) in subsequent statistical analyses. This conservative measure minimizes the effects of pseudoreplication and generates confidence in the outcomes (John Henstridge, Data Analysis Australia).

We scored the video and, for both species, recorded response variables to quantify approach and avoidance responses (Erhard et al. 2006): number of flights, number of approaches, number of animals entering the compound, and the number of animals entering the trough inside the compound. We counted the total number of animals sighted (events) in an evening. We also examined the number of events/approaches as a measure of the eagerness (and possible hunger status) of animals approaching the compound. Because some animals made many attempts to enter the compound when dingo urine was present, the overall success of the deterrent was measured as the number entering the compound/number of approaches taken to enter into the compound and the number of flights generated from the source cue. For possums, we also examined the number of animals that bypassed the treated gate and went over the fence to enter the compound. Weather (measured on a discrete scale of 1–3, with 1 indicating mild conditions, 2 indicating rain, and 3 indicating heavy rainfall and wind) was used as a covariate for all measures.

A linear regression model was fitted to each daily average (by hour) response with treatment as a predictor variable. We fitted a multivariate analysis of variance (MANOVA) and calculated Tukey's HSD for *post hoc* tests. Statistics were calculated using MiniTab version 15 (Chicago, IL, USA) and R v.2.11.0 statistical package (http://www.r-project.org). All tests were two-tailed; we set our $\alpha = 0.05$. Means are given ± SEM.

Results

Visitations were high for both species throughout trials (Fig. 2). Up to 10 possums and/or 5 pademelons were found within the enclosure at one time during control periods, additional animals of both species were often within camera view beyond the enclosure. For pademelons, the model was significant for treatment phase only (Before–During–After) (MANOVA: $F_{2,12} = 30.92$; p = 0.000), weather was not a factor (MANOVA: $F_{2,12} = 1.60$, p = 0.439). Pairwise comparisons for primary response variables (number entering compound, number entering trough, flights inside, flights outside) showed before and after phases to be similar, while the treatment phase was different (Fig. 3; Table 2).

The number of flights increased considerably at the compound entry when compared to the before and after phases ($F_{2,12} = 52.04$, p = 0.000; 1250% increase during treatment) and inside the trough area ($F_{2,12\ =}\ 6.73$, p = 0.000; there were no flights during either of the control phases). Our 'eagerness to feed' index (approaches/events) increased by 216% during treatments when animals repeatedly attempted to gain access inside the enclosure ($F_{2,12\ =}\ 18.71$, p = 0.001). The overall index of aversion (number of entries inside trough/approach to the compound; $F_{2,12}$ 147.1, p = 0.000) decreased from 90% prior to trials to 0.05% during the treatment phase (Fig. 3).

Prominent effect sizes (*d*-scores; Cohen 1988; Table 3) were obtained for differences between

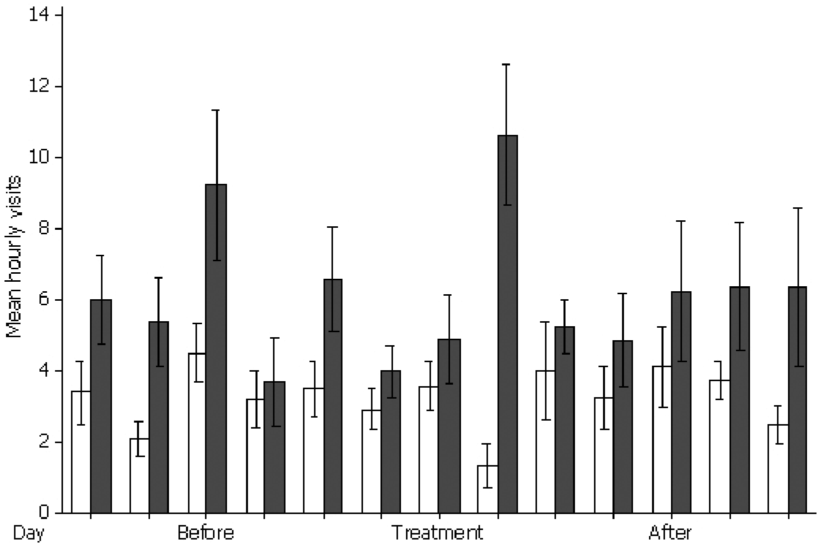

Fig. 2: Mean hourly visitations by brush tail possums (*Trichosurus vulpecula*) (shaded) and Tasmanian pademelons (*Thylogale billardierri*) to surveillance area before, during, and after the treatment period 25 Mar.–17 Apr. 2008.

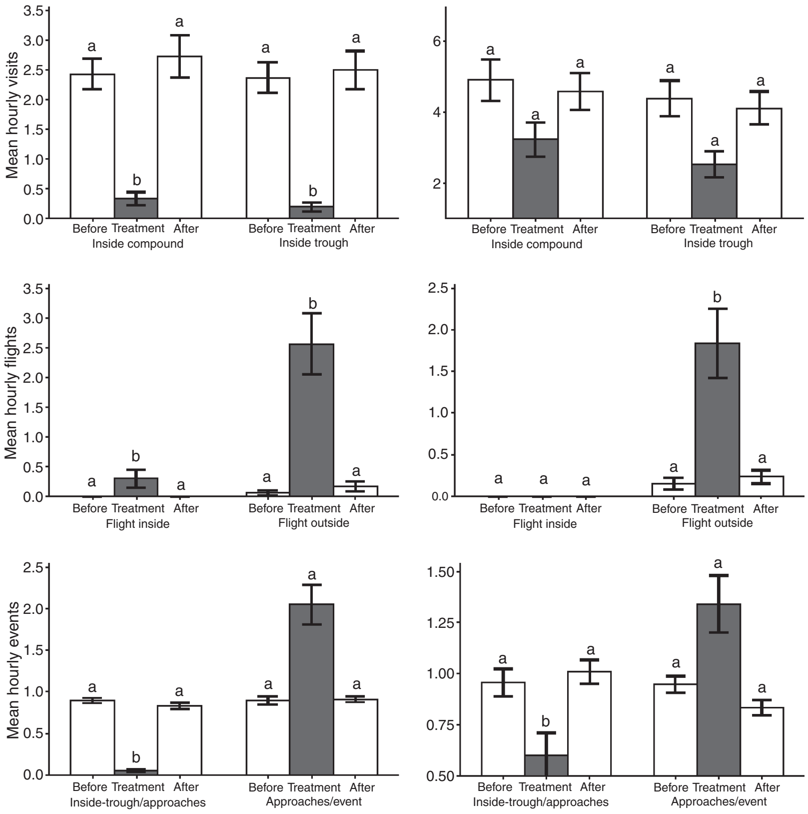

Fig. 3: Responses (X ± SEM) from *Thylogale billardierii* (left) to predator scent cues inside and outside exclosure compound and *Trichosurus vulpecula* (right). Different superscript letters differ significantly by Tukey's HSD test. Mean hourly flights were sqrt(X + 0.5)-transformed for statistical analyses.

Table 2: Aversive responses (X daily average/hour ± SEM) by pademelons (*Thylogale billardierii*) and brush tail possums (*Trichosurus vulpecula*) to dingo urine scent inside and outside an enclosure compound in Maydena, Tasmania

Species	Tasmanian pademelon		
Aversion index	Treatment Before	After–Before	After Treatment
Events (sightings recorded)	−0.78 ± 1.72, p = 0.4519	0.13 ± 1.49, p = 0.9689	0.91 ± 1.72, p = 0.3498
Approaches	1.8 ± 2.57, p = 0.1841	0.38 ± 2.23, p = 0.8858	−1.42 ± 2.57, p = 0.3279
Likelihood of hunger ratio (Approach/Sightings)	0.87 ± 0.39, **p = 0.0003**	0.06 ± 0.34, p = 0.8662	−0.81 ± 0.39, **p = 0.0005**
Successful entry (Inside trough/Approach)	−0.8 ± 0.16, **p = 0.000**	−0.08 ± 0.13,p = 0.2518	0.71 ± 0.16, **p = 0.000**
Entry Inside compound	−2.18 ±1, **p = 0.0004**	0.24 ± 0.86, p = 0.7433	2.42 ± 1, **p = 0.0002**
Entry inside trough	−2.24 ± 0.95**, p = 0.0002**	0.07 ± 0.82, p = 0.9704	2.31 ± 0.95,**p = 0.0001**
Flight trough	0.25 ± 0.2, **p = 0.0151**	0 ± 0.17, p = 1	−0.25 ± 0.2, **p = 0.0151**
Flight compound	2.38 ± 0.71, **p = 0.000**	0.09 ± 0.62, p = 0.9252	−2.3 ± 0.71, **p = 0.000**
Entry over fence	–	–	–
	Brush tail possum		
Events (sightings recorded)	0.34 ± 4.22, p = 0.9739	−0.37 ± 3.66,p = 0.9598	−0.7 ± 4.22, p = 0.8929
Approaches	1.21 ± 3.16, p = 0.5656	−1.08 ± 2.74,p = 0.5490	−2.28 ± 3.16,p = 0.1676
Likelihood of hunger ratio (Approach/Sightings)	0.28 ± 0.38, p = 0.1540	−0.12 ± 0.33,p = 0.6124	−0.4 ± 0.38, p = 0.0403
Successful entry (Inside compound/Approach)	−0.38 ± 0.25, **p = 0.0055**	0.09 ± 0.22, p = 0.5122	0.47 ± 0.25, **p = 0.0012**
Entry inside compound	−1.38 ± 2.63, p = 0.3602	−0.42 ± 2.27,p = 0.8728	0.96 ± 2.63, p = 0.5915
Entry inside trough	−1.65 ± 2.23, p = 0.1552	−0.36 ± 1.93,p = 0.8677	1.29 ± 2.23, p = 0.2948
Flight trough	0	0	0
Flight compound	1.6 ± 0.55, **p = 0.000**	0.11 ± 0.48, p = 0.8081	−1.49 ± 0.55, **p = 0.0001**
Entry over fence	0.24 ± 0.45, p = 0.3531	0.01 ± 0.39, p = 0.9973	−0.23 ± 0.45, p = 0.3816

Comparisons are between before, during treatment, and after phases. Bold p values differ significantly by Tukey's HSD test.

Table 3: Measures of effect (*d*-scores) comparing the response of pademelons (*Thylogale billardierii*) and brush tail possums (*Trichosurus vulpecula*) to dingo urine scent inside and outside enclosure compound in Maydena, Tasmania

Species	Response	Before Treatment	After Treatment	Before–After
Pademelon	Enter compound	6.16	7.35	−0.82
	Trough	7.51	6.48	−0.08
	Flights in	−1.78	−1.58	0
	Flights out	−1.79	−1.44	−0.71
	Trough/approach	1.00	11.49	0.60
	Approach/sighting	−3.29	−2.25	−2.41
Possum	Enter compound	1.30	0.62	1.04
	Trough	1.93	1.22	1.10
	Flights in	0	0	0
	Flights out	−2.64	−2.28	−0.37
	Trough/approach	2.63	3.15	−0.79
	Approach/sighting	−1.05	−1.42	1.49

number of animals entering the compound, entering the trough and number of flights inside and outside the compound, when compared to the control phases.

For possums, the MANOVA was significant for the treatment phase (MANOVA: $F_{2,12} = 5.988$, p = 0.002). Weather did not significantly affect behaviour (MANOVA: $F_{2,12} = 1.27$, p = 0.335). Pairwise comparisons for all response variables showed before and after phases to be similar, while the treatment phase was different (Fig. 3, Table 2). There were no flights from the trough at any time before or during treatments, although there were many flights at the enclosure entry ($F_{2,12} = 36.42$, p = 0.000; 963% increase during treatments). Entries over the fence (as a bypass to the gate) increased by 34% during the treatment phase, though not significantly so ($F_{2,12} = 1.25$, p = 0.329). Our 'eagerness to feed' measure (approaches/events) increased by 75% during the treatment phase, and the overall index of aversion (number animals that entered trough/number approaches to the compound) dropped from 95% prior to treatments to 60% during treatments ($F_{2,12} = 13.65$, p = 0.001). Prominent effect sizes (*d*-scores; Cohen 1988; Table 3) were obtained for differences between the number of flights outside the compound and the aversive index inside trough/approach, when compared to the control phases.

Discussion

Both pademelons and possums demonstrated fear-based aversions to the novel scent, despite having no previous experience with dingoes. Scents outside the compound deterred both species similarly, however, inside the compound species reacted differently: pademelons took flight from both scent barriers, while the possums only took flight outside the compound. Pademelons may have been more 'vulnerable' inside the enclosure because they are a ground-dwelling species, while the arboreal possums had the ability to escape if cornered inside the facility. These findings suggest that experimental enclosures can act as an indirect fear cue similar to other factors (moonlight, distance from shelter, reduced vegetation) indicating vulnerability (Orrock & Danielson 2004; Orrock et al. 2004; While & McArthur 2005; Preisser et al. 2007; Liley & Creel 2008). Interestingly, if we had chosen to only guard the trough and not the entry to the compound, we might have underestimated the effect the scent had on the possum behaviour.

Responses from both possums and pademelons to novel dingo scents do not provide any insight as to why mainland marsupials are so susceptible to novel predators. Our findings are in contrast to Mcevoy et al. (2008) who concluded that Tasmanian fauna are not capable of responding to the novel scent and therefore are vulnerable to exotic predators (such as the red fox (*Vulpes vulpes*). Ultimately, both of these species of marsupials are able to respond to the scent of a novel predator. These outcomes differ from our previous findings with western grey kangaroos, which exhibited marginal responses (but no flights) to novel coyote scent (Parsons et al. 2007). Perhaps, dingo scent is inherently more volatile, complex, or concentrated than that of coyotes.

Based on the high turbidity of the dingo urine, it is likely that dingoes produce more concentrated urine than either of the novel predators previously reported by Mcevoy et al. (2008) or Parsons et al. (2007). These findings are consistent with studies where small prey demonstrate a *leitmotif* response to 'general' predators (Apfelbach et al. 2005). In the case of Parsons et al. (2007), the results may be explained by the relative body sizes of predator and prey; both Tasmanian species were much smaller than western grey kangaroos. Gelparin (2008) and Brennan (2009) imply that prey could potentially be able to ascertain enough information from the urine to detect differences in body mass; thus, small prey may be more susceptible to a *leitmotif* response than larger prey. The response to the novel dingo scent may also be linked to evolutionary coexistence of pademelons and possums to the predatory thylacine (*Thylacinus cynocephalus*), an extinct, canid-like marsupial carnivore, or to the coexistence with

Tasmanian devils and quolls. However, both Gelparin (2008) and Brennan (2009) imply that olfactory abilities are too well developed for prey to confuse urine from one predator species with another.

Our results highlight Mcevoy et al.'s (2008) comment about the necessity of choosing the proper index of assessment when studying olfactory predator discrimination. By examining the ratio of the number of approaches taken to enter the compound against the number of recorded events, we found evidence of a high persistence of the animals in taking food that was much better than that available in the surrounding environment. The overall index of deterrence (number of approaches/number of successful feeds from the trough) proved useful in demonstrating the difference in success in reaching the food.

Conclusions

Pademelons and brush tail possums exhibit fear-based aversions to urine from dingoes, an allopatric species, despite the lack of historical interactions between them. Indirect risk cues, such as perceived shelter, may impact the overall efficacy of a danger cue when attempting to repel brush tail possums, but not Tasmanian pademelons. The contrasting effects of possums inside and outside the enclosure illustrate the need for applying kairomones in the appropriate context when using them as olfactory-based repellents. We suggest the cumulative, or counter, effects of indirect and direct risk cues must be considered when dispersing all potential fear-based repellents. Our findings may also be relevant for conservation interests, particularly if small animals that have not learned a fear of *specific* predators may be conditioned to avoid general (*leitmotif*) predators they have not previously been in contact with.

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