

Olfactory predator recognition: wallabies may have to learn to be wary

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Abstract

Many species modify their behaviour in response to the scents of their predators, but species or populations living without predators may lose such abilities. This loss has been suggested to be irreversible, and to constitute a significant hurdle in restoring historical ecosystems. Olfactory predator recognition was studied in two macropodid marsupials – the tammar wallaby (*Macropus eugenii*) and the red-necked pademelon (*Thylogale thetis*). Both species are in the ‘critical weight range’ of Australian native mammals that have been negatively affected by the introduction of novel predators since European settlement. Predator-naïve animals were tested by exposing subjects simultaneously to two feeders with either a predator or a herbivore faecal or urine sample beneath the food tray. The presence of predator olfactory cues beneath the feeder did not affect foraging behaviour or feeder use when compared to control stimuli (herbivore faeces or urine). Previous studies have found that predator-experienced herbivorous marsupials modify their behaviour in the presence of predator scents. In contrast, our studies of predator-naïve individuals found no evidence of such selectivity, suggesting that marsupial herbivores may have to learn to modify their behaviour in response to olfactory cues from predators. This implies that the loss of olfactory predator recognition may not be irreversible. Animals translocated from predator-free areas could potentially be trained to recognise the smells of their predators.

INTRODUCTION

In addition to numerically reducing prey populations, predators have a remarkable variety of indirect effects on their prey (Wootton, 1994). Individuals in the presence of predators often forage less and are more vigilant, or simply choose to forage elsewhere (Lima & Dill, 1990). Such indirect effects may have profound consequences if a prey population exhibits density-dependent growth (Gill, Sutherland & Watkinson, 1996; Gill & Sutherland, 2000). The effects of predators are mediated by each species’ ability to identify them. Prey species commonly detect predators by sight, sound and smell.

While it may seem logical for predator recognition abilities to be more-or-less experience-independent (i.e., to be ‘hard wired’), species from a number of taxa can learn to recognize their predators (review in Griffin, Blumstein & Evans, 2000). However, there is no reason to believe that developmental plasticity in one modality (e.g., vision) necessarily implies a similar role for experience in another (e.g., olfaction).

One powerful way to understand the mechanisms underlying recognition abilities is to study individuals from populations with different ontogenetic and evolutionary histories of exposure to predators. By comparing individuals living with predators in the wild to predator-naïve captive-bred individuals, we can identify the degree to which experience is important for predator recognition. Additionally, because antipredator behaviour is often costly, we expect it to be lost over evolutionary time in predator-free populations (Coss, 1999; Magurran, 1999). By comparing populations or

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species living under different predation regimes, we can thus make inferences about the time course of relaxed selection (Berger, 1999; Coss, 1999).

The sight of an individual predator reveals that predators are present in a particular part of an animal's range and may also provide behavioural cues about the probability of attack. Prey may respond, without prior experience, to some visual cues (Curio, 1966). For instance, tamar wallabies (*Macropus eugenii*) from a population that has been isolated from mammalian predators for 9500 years respond to the sight of novel predators (Blumstein *et al.*, 2000). Convergent evolution has made large carnivores morphologically similar, and prey may have been selected to respond to a few key shared features. This would allow visual predator recognition to persist after many generations of relaxed selection (Blumstein *et al.*, 2000).

While hunting, predators often remain quiet, yet they too must communicate with conspecifics and social carnivores often use acoustic signals. Vulnerable prey species might potentially use these cues to modify their behaviour appropriately. In contrast to morphology, however, acoustic signals are often species specific, and evidence to date is consistent with the hypothesis that prey may have to learn the sounds of their predators (Blumstein *et al.*, 2000).

All carnivores produce similar sulfurous metabolites from meat digestion (Nolte *et al.*, 1994), suggesting that prey might be selected to recognize these convergent olfactory features. Evidence for experience-independent olfactory predator recognition is variable. For instance, California ground squirrel (*Spermophilus beecheyi*) populations, isolated from rattlesnake predators for 70,000–300,000 years, retain the ability to respond to the scent of rattlesnakes (*Crotalus* spp.; Coss, 1999), as do meadow voles (*Microtus pennsylvanicus*) isolated from their mustelid predators for 10,000 years (Parsons & Bondrup-Nielsen, 1996). However, predator-naïve populations of other rodents, fish and ungulates fail to respond to the scent of predators (e.g., Magurran, 1989; Kavaliers, 1990; Berger, 1998), and there are suggestions that predator-related olfactory stimuli may generally have to be learned (Beauchamp, 1997). Numerous experiments have demonstrated that fish quickly learn to respond to the smells of their predators (e.g., Magurran, 1989; Chivers & Smith, 1995), and this process may be facilitated by an evolutionary history of exposure to predators (Magurran, 1990). Experience-dependent olfactory predator recognition may be functional in that the scent of a predator alone may provide limited information on the probability of predation. Olfactory cues may persist long after the animal responsible for the smell has left the area (Bradbury & Vehrencamp, 1998). Animals using olfactory cues are likely to make errors in estimating predation risk (Bouskila & Blumstein, 1992) and, because increased vigilance would be triggered by all carnivore scents rather than only those of potential predators, these costs might be sufficient to select for selectively learning predator smells.

The mechanisms underlying predator recognition, and

the degree to which they vary by modality, have important consequences for conservation biologists and restoration ecologists. The recent increase in global extinction has been particularly effective at reducing the numbers of terrestrial carnivores – particularly large ones (Berger, 1999; Woodroffe & Ginsberg, 2000) – and the loss of these important predators may have profound effects on the structure and function of the communities in which they lived (Berger, 1999). For those interested in reintroducing species (Kleiman, 1989), or in restoring functioning ecosystems (Young, 2000), the mechanisms underlying recognition are particularly relevant. Learned mechanisms can presumably be re-acquired with sufficient experience, while the loss of more hard-wired mechanisms after some period of relaxed selection would be more difficult to address.

Australia has the world's worst record of recent mammalian extinctions (Flannery, 1994) affecting both native predators and prey (Maxwell, Burbidge & Morris, 1996). Many populations of prey species exist in predator-free reserves or on predator-free offshore islands. There is a great interest in restoring historical Australian mammalian communities and there have been a number of reintroductions and translocations for conservation (Short *et al.*, 1992; Serena & Williams, 1995). In Australia, as elsewhere (Wolf *et al.*, 1996), many of these attempts have failed, and predation by introduced novel predators has been implicated as a major cause (McCallum, Timmers & Hoyle, 1995).

While considerable information has been collected on olfactory predator recognition in eutherian mammals (Kats & Dill, 1998), much less is known about marsupials. We studied olfactory predator recognition in two small macropodid marsupials by exposing them to the faeces of carnivores and herbivores. We used either wild-caught or captive-bred tamar wallabies (from Kangaroo Island, South Australia), and captive-bred red-necked pademelons (*Thylogale thetis*) from New South Wales. These species were selected because while Kangaroo Island tammars have a rich evolutionary history of exposure to marsupial predators – thylacinids (marsupial lions/tigers) and dasyurids (quolls, tiger cats and devils); (Archer, 1981; Robertshaw & Harden, 1989) – they have not been exposed to mammalian predators since ice age sea level changes isolated the island from the mainland 9500 years ago (Lampert, 1979; Blumstein *et al.*, 2000). European settlers introduced cats (*Felis catus*) and dogs (*Canis familiaris*) in the past century, but these species are largely restricted to areas around human settlement. In contrast, free-living red-necked pademelons have a continuous history of exposure first to marsupial predators (the same thylacinids and dasyurids as tammars), then to dingoes (*Canis lupus dingo*; Corbett, 1995), and most recently to foxes, cats and dogs (Strahan, 1995). Thus, we have predator-naïve individuals (wild-caught or captive-bred) from a species with only distant historical experience with predators (tammars), and predator-naïve individuals from a species with more recent exposure to predators (pademelons). The two species were also selected because they are

both within the 'critical weight range' (Burbridge & McKenzie, 1989) of Australian mammals that have suffered population declines and extinctions following European settlement (tamar females are about 5.5 kg: Smith & Hinds, 1995; pademelon females are about 3.8 kg: Johnson, 1995). Tammars are now extinct on mainland South Australia (Smith & Hinds, 1995) and there are plans to recover this population by reintroduction and translocation. Western Australian tammars are now restricted to a few isolated populations (Morris *et al.*, 1998). We compare the results from our study to those reported in the literature for other marsupials to test the general hypothesis that macropodids have an innate ability to recognise their predators.

METHODS

Subjects and experimental area

Twenty-eight captive-born or wild-caught predator-naïve tamar wallabies (25 females, 3 males) from Kangaroo Island and 16 captive-born predator-naïve red-necked pademelons (8 females, 8 males) were selected from the breeding colony at the Macquarie University Fauna Park. Prior to the experiment, subjects lived in mix-sex aggregations in outdoor enclosures where they could forage on natural vegetation and were provided supplemental kangaroo pellets *ad libitum* (Gordon's Stockfeed) and water. Our wild-caught tammars were captured in western Kangaroo Island and are likely to have had no experience with either cats or dogs before capture. All pademelons, and some tammars were captive-bred. Once in captivity, subjects may have seen cats – which were occasionally seen passing through the Fauna Park; dogs were completely excluded by the double fences surrounding the park.

Four subjects were simultaneously tested in a 16 × 14 m outdoor experimental enclosure subdivided into four triangular testing arenas (each about 28 m²; Fig. 1). Most subjects quickly habituated to their new surroundings; one pademelon was removed from the experiment after escaping into an adjacent enclosure on two consecutive days.

A four-channel video surveillance system (WOOGU model L-8525) recorded activity around the two identical feeding bins in each yard, beneath which we placed the olfactory stimuli. Each bin was surrounded by white bricks positioned in a semi-circle 1 m in diameter. This allowed the person scoring the videotape to determine accurately when a subject was within 1 m of a particular bin. These data were used to measure the spatial distribution of feeding for each animal to establish whether it was avoiding a particular olfactory stimulus.

Olfactory stimuli and hypotheses

We obtained faecal samples from carnivores (red fox, (*Vulpes vulpes*), kodiak bear (*Ursus arctos*) and dingo) – all of which were fed a diet that included meat – and from herbivores (camel (*Camelus dromedarius*), horse (*Equus caballus*), giraffe (*Giraffa camelopardalis*) and

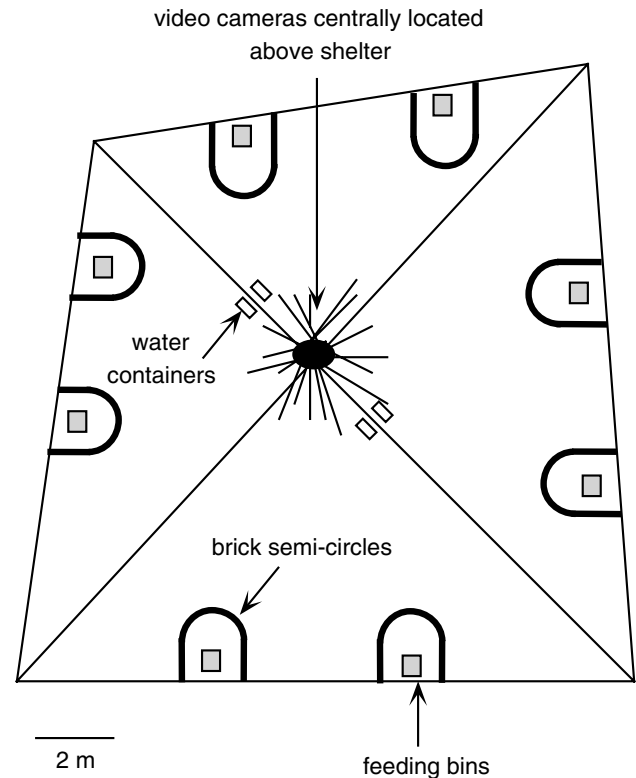


Fig 1. Illustration of the experimental testing arenas used to study olfactory predator recognition.

elephant (*Elaphas maximus*)). All predator stimuli were unfamiliar to our predator-naïve subjects. One analysis suggested that tammars either avoided carnivores or were attracted to novel herbivores (see Discussion). We therefore report an additional treatment of carnivore versus a familiar herbivore (tamar wallaby faeces). For both tammars and pademelons, all other herbivores were unfamiliar. We also obtained urine samples from an unfamiliar carnivore (domestic dogs) and an unfamiliar herbivore (human vegans). Faeces and urine were frozen at -20°C on the day of collection. We weighed 10 g of faeces and stored them in 40 ml plastic specimen jars. On the day of use, each faecal sample was hydrated with 5 ml deionised water to make a thick and pungent slurry. Urine (10 ml) was stored frozen in 40 ml specimen jars and thawed on the day of use. To our noses, different samples produced distinctive odours.

We tested the following five hypotheses:

- H1 Tammars do not discriminate between the faeces of unfamiliar carnivores and unfamiliar herbivores.
- H2 Tammars do not discriminate between the faeces of unfamiliar carnivores and familiar herbivores (tamar).
- H3 Tammars do not discriminate between the urine of unfamiliar carnivores (dog) and unfamiliar herbivores (human vegan).
- H4 Pademelons do not discriminate between the faeces of unfamiliar carnivores and unfamiliar herbivores.

H5 Pademelons do not discriminate between the urine of unfamiliar carnivores (dog) and unfamiliar herbivores (human vegan).

General experimental design

Olfactory stimuli were presented to tammars in simultaneous choice tests between two bins, one of which had a carnivore and the other a herbivore sample beneath it. This design maximizes our ability to detect whether subjects can discriminate between classes of stimuli (e.g., carnivores versus herbivores) but does not permit us to make direct comparisons among different stimuli (e.g., one carnivore versus another). Urine and faecal samples were randomly assigned to food bins to eliminate the probability of spatial confounds. The order of stimulus presentation was randomized for each individual within each experimental block. We used a series of preliminary trials to try to remove feeder biases by moving the location of protective cover in each arena so that it was equidistant from both feeders. For the pademelon experiment, we eliminated feeder bias experimentally by testing each subject with both stimuli twice, reversing the bins under which the stimuli were presented the second time, and averaging the two scores.

Animals were habituated to the experimental yards for 3 days prior to beginning the experiment. During this time, we opened the feeding bins 3 hours before sunset and closed them just after sunset. On the experimental days, the video cameras were switched on prior to a researcher entering the enclosures to place a stimulus beneath each feeder, and to open all feeders.

Trials were scored blind with respect to treatment. We noted the frequency with which a subject came within 1 m of the feeder (defined by the brick semi-circle; Fig. 1) and the duration of time each subject remained within this area. From the raw data, the following measures were obtained: (a) total time spent around each feeder as a proportion of the total observation time; (b) time spent around each feeder as a proportion of the total time in both feeder areas; (c) average duration of a visit; (d) number of visits to a bin each hour; (e) latency to visit each feeder.

Data manipulation and statistical analyses

We excluded from analysis animals that did not visit the feeders during filming or escaped from our testing arenas. One tamarin never fed during the test of H3 and was excluded from analysis. Two pademelons were excluded from analysis: one escaped from the experimental arena, and the other never visited the feeders during filming. Additionally, there were a few cases when technical difficulties prevented us from recording the exact time the feeders were opened. This affected only the latency to feeding measure, so we excluded these trials from that analysis.

Individual variation was great; all data were skewed and treatments had non-homogeneous variances. We used non-parametric Wilcoxon–Signed Rank tests to test

the hypotheses that bin visitation was unaffected by the presence of a predator's smell. We report two-tailed *P*-values and use an α level of 0.05 throughout. Statistics were calculated using Statview 5.1 (SAS Institute, 1998).

RESULTS

Feeder choice for tammars and pademelons was largely unaffected by the test stimuli (Table 1). The only exception to this generalization was the test of hypothesis 1 – unfamiliar carnivore vs. unfamiliar herbivore faeces. Tammars foraged more and had significantly longer bouts of foraging at the bin containing the unfamiliar herbivore faecal sample. There were no significant differences between treatments for the other variables, and some of the larger non-significant differences were in the direction opposite that predicted if animals were actively avoiding predator smells. For instance, while not significant, pademelons spent more time foraging next to dog urine, and tammars had longer foraging bouts next to dog urine than vegan urine.

DISCUSSION

Marsupials have a well-developed olfactory system and produce a variety of olfactory secretions used in social contexts (Salamon, 1996). However, the foraging behaviour of both tammars and red-necked pademelons was not affected by the presence of predator faeces or urine beneath a feeder. The only exception to this generalization occurred when testing the first hypothesis; tammars foraged more next to the unfamiliar herbivore faeces. Since there were no differences between the carnivore and the familiar herbivore treatments, we conclude that tammars were not repelled by the presence of carnivore faeces. Our interpretation is rather that tammars were attracted to the largely undigested grass contained in the elephant, horse and camel faeces. It is possible that the results of other studies of herbivore–predator discrimination that rely on time budgets to quantify discrimination (as opposed to obvious alarm responses) could be interpreted similarly. Note that we were able to differentiate between many of these smells at the distance at which the animals fed, and marsupial olfactory sensitivity exceeds that of humans (Salamon, 1996). This failure to adjust feeding behaviour in response to olfactory cues from predators contrasts with reports of similar effects in other species. Tamarin wallabies have been observed to forage closer to cover in high-risk habitats so they clearly have the ability to respond to some predator-risk cues (D. T. Blumstein & J. C. Daniel, unpublished data). We conclude that the scent of predators did not affect foraging behaviour in either tammars or pademelons.

Decisions animals make about where and how to forage occur after stimulus detection (Blumstein & Bouskila, 1996). We are currently unable to determine whether the absence of a foraging inhibition response reflects the inability to detect differences between the olfactory stimuli, or whether the animals did not

Table 1. Results (\pm SD) of paired feeder preference trials. All carnivores' scents were unfamiliar to our predator-naïve individuals. Significant *P*-values are in bold. Sample sizes for the different hypothesis tests are: H1, *N* = 16; H2, *N* = 16; H3, *N* = 11; H4, *N* = 14; H5, *N* = 14.

	Carnivore	Herbivore	<i>P</i> -value
% of total observation time			
H1 Tammar: carnivore–unfamiliar herbivore faeces	8.0 (\pm 7.5)	16.3 (\pm 10.0)	0.05
H2 Tammar: carnivore–familiar herbivore faeces	8.8 (\pm 11.6)	13.7 (\pm 10.1)	0.26
H3 Tammar: carnivore–unfamiliar herbivore urine	10.3 (\pm 9.6)	8.6 (\pm 9.1)	0.72
H4 Pademelon: carnivore–unfamiliar herbivore faeces	8.8 (\pm 6.1)	7.7 (\pm 4.0)	0.93
H5 Pademelon: carnivore–unfamiliar herbivore urine	9.8 (\pm 6.3)	8.0 (\pm 4.6)	0.64
% of total feeding time			
H1 Tammar: carnivore–unfamiliar herbivore faeces	37.6 (\pm 34.1)	62.4 (\pm 34.1)	0.16
H2 Tammar: carnivore–familiar herbivore faeces	36.1 (\pm 37.2)	63.9 (\pm 37.2)	0.14
H3 Tammar: carnivore–unfamiliar herbivore urine	53.3 (\pm 38.4)	46.7 (\pm 38.4)	0.72
H4 Pademelon: carnivore–unfamiliar herbivore faeces	52.8 (\pm 13.8)	47.2 (\pm 13.8)	0.42
H5 Pademelon: carnivore–unfamiliar herbivore urine	56.5 (\pm 20.8)	43.5 (\pm 20.8)	0.21
Average duration (min)			
H1 Tammar: carnivore–unfamiliar herbivore faeces	3.0 (\pm 21.8)	5.3 (\pm 3.3)	0.04
H2 Tammar: carnivore–familiar herbivore faeces	2.5 (\pm 2.6)	3.5 (\pm 2.3)	0.23
H3 Tammar: carnivore–unfamiliar herbivore urine	5.5 (\pm 4.6)	3.6 (\pm 3.0)	0.37
H4 Pademelon: carnivore–unfamiliar herbivore faeces	5.1 (\pm 4.2)	4.6 (\pm 3.4)	0.36
H5 Pademelon: carnivore–unfamiliar herbivore urine	4.9 (\pm 4.1)	5.5 (\pm 4.2)	0.59
N bouts/hr			
H1 Tammar: carnivore–unfamiliar herbivore faeces	1.6 (\pm 1.3)	1.7 (\pm 0.8)	0.53
H2 Tammar: carnivore–familiar herbivore faeces	1.5 (\pm 1.4)	2.5 (\pm 1.9)	0.22
H3 Tammar: carnivore–unfamiliar herbivore urine	1.0 (\pm 0.6)	1.2 (\pm 1.1)	0.65
H4 Pademelon: carnivore–unfamiliar herbivore faeces	1.2 (\pm 0.8)	1.1 (\pm 0.6)	0.98
H5 Pademelon: carnivore–unfamiliar herbivore urine	1.4 (\pm 0.9)	1.0 (\pm 0.6)	0.06
Latency to feed (min)			
H1 Tammar: carnivore–unfamiliar herbivore faeces	57.1 (\pm 64.3)	23.8 (\pm 38.8)	0.15
H2 Tammar: carnivore–familiar herbivore faeces	44.7 (\pm 73.2)	30.0 (\pm 49.1)	0.8
H3 Tammar: carnivore–unfamiliar herbivore urine	56.3 (\pm 67.0)	80.9 (\pm 74.0)	0.48
H4 ¹ Pademelon: carnivore–unfamiliar herbivore faeces	63.2 (\pm 46.7)	86.0 (\pm 34.7)	0.13
H5 ² Pademelon: carnivore–unfamiliar herbivore urine	42.3 (\pm 41.5)	60.8 (\pm 54.6)	0.09

¹*N* = 11, ²*N* = 10

modify their foraging behaviour because predator scents were not salient, although we think the latter possibility more likely. A better understanding of this phenomenon would require a behaviour-independent assay (e.g., cardiac responses – see Evans & Gaioni, 1990; Blumstein & Bouskila, 1996).

It is possible that the cost of a mistake for captive animals in a predator-free environment is less than for wild animals and that captive subjects are more 'relaxed' and therefore less likely to discriminate. We consider this unlikely. Captive tammar discriminate among the predators using visual cues (Blumstein *et al.*, 2000) and exhibit group-size effects that suggest that they are sensitive to variation in the risk of predation (Blumstein, Evans & Daniel, 1999).

A compilation of other work on predator recognition in marsupial herbivores put these results into perspective (Table 2). All studies of predator-experienced individuals found evidence that they modified their behaviour in the presence of predator scents. In contrast, studies of predator-naïve individuals have found no evidence of differential behaviour when exposed to such olfactory cues. Our pademelon result is particularly important because it demonstrates that as little as a generation or so of captive-living may be sufficient for a species to stop responding to predator scents. Taken together, these results suggest that marsupial herbivores learn to modify their behaviour in response to olfactory cues that predict the presence of predators.

Table 2. Summary of studies on olfactory predator recognition in herbivorous marsupials. The first three species are macropodids.

Species	Predator experience	Responds to the scent of predators?	Reference
Tammar wallaby (<i>Macropus eugenii</i>)	Evolutionary ¹ Not ontogenetic	No	This study
Red-necked pademelon (<i>Thylogale thetis</i>)	Evolutionary ² Not ontogenetic	No	This study
Swamp wallaby (<i>Wallabia bicolor</i>)	Evolutionary and ontogenetic ³	Yes	Montague, Pollock & Wright, 1990
Brushtail possum (<i>Trichosurus vulpecula</i>)	Evolutionary and ontogenetic ⁴	Yes	Morgan & Woolhouse, 1997; D. Morgan, pers. comm.
Brushtail possum	Evolutionary and ontogenetic ⁵	Yes	Gresser, 1996

¹Kangaroo Island tammar were last exposed to natural mammalian predators about 9500 years ago.²Red-necked pademelons were last exposed to mammalian predators before being brought into captivity – one or two generations ago.³Field study on predator-experienced wallabies.⁴Wild-caught, predator-experienced possums.⁵Field study on predator-experienced possums.

Fortunately, it seems that many species can be taught about the predators they are likely to encounter (McLean *et al.*, 2000), that the lessons they learn about one predator might be generalizable to other similar predators

(Griffin, Evans & Blumstein, 2001), and that learning may be rapid (Berger, Swenson & Persson, 2001). For example, a number of Australian marsupials have been trained to respond adaptively to predators to which they previously showed little response (McLean *et al.*, 2000). By either pairing the presentation of a model predator with an aversive event, or by using a live muzzled dog as an inherently aversive stimulus, rufous bettongs (*Aepyprymnus rufescens*), rufous hare-wallabies (*Lagorchestes hirsutus*) and quokkas (*Setonix brachyurus*) learned to respond fearfully, or were trained to produce a novel antipredator behaviour (running to a refuge), in response to the presence of a canid. Recent work in our laboratory has demonstrated not only that tamar wallabies can be trained, but also that training with one predator increases response to similar, non-trained, predators (Griffin *et al.*, 2001). Specifically, tammars trained to increase their responsiveness to foxes also showed a sustained response to cats (another potential predator), but not to non-predators (wallabies and goats). Moreover, the subjects in these studies required only a few training sessions to acquire fear of novel predators. Thus, predator training may be a cost-effective way to help increase survival of potentially vulnerable prey by teaching them to respond specifically to predators. Finally, several studies have demonstrated the practical benefits of this approach; predator training can increase the survival of reintroduced individuals (Ellis, Dobrott & Goodwin, 1977; van Heezik, Seddon & Maloney, 1999).

If experience is important for marsupials to learn about the scents of their predators, it is possible that contextual conditioning methods (Domjan & Burkhard, 1985) could be used to inculcate wariness prior to translocation into predator-rich areas. Briefly, contextual conditioning occurs when an individual is trained to associate an experimental setting, rather than a specific stimulus, with an aversive event. In many such experiments, it is necessary to incorporate a 'safe' area in the design that lacks the contextual cue with which training is being attempted. For example, this approach might be implemented by spreading fox faeces around part of an enclosure and then exposing animals to a fear-inducing stimulus only when they moved into that area. The alternative approach of pairing a pulse of fox odour with an aversive event is theoretically promising, but it may prove difficult in practice because olfactory cues do not have the punctate temporal characteristics of visual or acoustic stimuli.

The mechanism by which species assess predation risk has important implications for conservation. For instance, our results suggest that concern about the loss of interspecific processes involving animal behaviour (Berger, 1999) is only an issue for those behaviours truly 'lost' by relaxed selection, and not for those experience-dependent behaviours not performed because of impoverished ontogeny. The combination of our results with those obtained in other studies of marsupial herbivores predicts that olfactory predator recognition abilities may be restored following isolation from predators.

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