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Antipredator behaviour of red-necked pademelons: a factor contributing to species survival?

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Abstract

Australian mammals have one of the world's worst records of recent extinctions. A number of studies have demonstrated that red foxes (*Vulpes vulpes*) have a profound effect on the population biology of some species. However, not all species exposed to fox predation have declined. We studied the antipredator behaviour of a species that has not declined – the red-necked pademelon (*Thylogale thetis*), and contrasted it with previous studies on a species that has declined – the tammar wallaby (*Macropus eugenii*), to try to understand behavioural factors associated with survival. We focused on two antipredator behaviours: predator recognition and the way in which antipredator vigilance is influenced by the presence of conspecifics. We found that predator-naïve pademelons responded to the sight of certain predators, suggesting that they had some degree of innate recognition ability. However, pademelons responded similarly to a broad range of acoustic stimuli, including dingo howls, wedge-tailed eagle calls, foot-thumps – a predator-elicited sound – and a control sound, suggesting that they did not specifically recognize predator vocalizations. Unlike a number of other macropodid marsupials, including tammars, pademelons did not modify time allocated to antipredator vigilance as group size increased. Taken together, these results suggest that red-necked pademelons independently assessed and managed their predation risk whereas tammars relied more on conspecifics to assess and manage risk. We suggest that these factors may have been important determinants of species survival. More generally, we suggest that a fundamental understanding of antipredator behaviour can enlighten conservation efforts.

INTRODUCTION

Since European settlement, 19 small and mid-sized Australian marsupials and native rodents have become extinct (Burgman & Lindenmayer, 1998), and many more are either threatened or endangered (Burbidge & McKenzie, 1989). The cause of this decimation is complex and likely to be multi-factorial; landscape changes associated with agriculture, the change in Aboriginal burning regimes, and the introduction of exotic competitors and predators are all implicated (Johnson, Burbidge & McKenzie, 1989; Flannery, 1994; Kohen, 1995). While dingoes (*Canis lupus dingo*) came to Australia about 3500 years ago (Corbett, 1995), the European introduction of cats (*Felis catus*; Low, 1999), and especially foxes (Coman, 1995; Short, Kinnear & Robley, 2002), seems to have been particularly destructive.

Several lines of evidence suggest that predation by foxes may be associated with local extinctions. First, widespread selective removal of foxes in parts of Western Australia has led to a resurgence in the numbers of native mammals (Morris *et al.*, 1998). Second, Tasmania, an island isolated from the Australian mainland for about 9500 years and subjected to recent habitat modifications, has cats but not foxes, yet contains a reasonably intact mammalian community which includes a number of species either critically endangered or extinct on the Australian mainland (Watts, 1993).

Not all species have declined or become extinct on the mainland. Although canids (foxes and dingoes) may reduce recruitment rates of kangaroos and the larger wallabies (Banks, Newsome & Dickman, 2000; Pople *et al.*, 2000), these large-bodied species typically have benefited from the construction of watering holes and pasture improvements for livestock that accompanied European settlement (Flannery, 1994; Burgman & Lindenmayer,

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1998). One exception to the general body-size pattern is the red-necked pademelon (*Thylogale thetis*) which, although relatively small, is not endangered (Maxwell, Burbidge & Morris, 1996). In fact, in parts of its mainland range, it is perceived by some as an agricultural pest (Johnson, 1977).

Red-necked pademelons are 4–7 kg macropodid marsupials that live along the rainforest edge in subtropical eastern Australia (Johnson, 1980). In some areas, rainforest clearing has led to an increase in forest edge adjacent to pasture, and has resulted in a population increase (Johnson, 1977). Other similarly sized forest edge species, such as the tammar wallaby (*Macropus eugenii*) (4–10 kg), have not fared well; landscape modifications and predation are implicated in the tammar's extinction from mainland South Australia, and fox removal in Western Australia has 'recovered' a nearly extinct mainland population (Morris *et al*., 1998).

What is it that makes these two species differentially vulnerable to similar factors? Part of the answer is probably ecological: foxes have not penetrated the dense rainforest as effectively as they have other habitat types in Australia (Coman, 1995), such as the coastal scrub and dry sclerophyll forests that are home to tammars (Smith & Hinds, 1995). But there are likely to be other reasons.

The ability to respond adaptively around predators has profound implications for coexistence of predators and prey following range expansions, such as those that occur in response to climate change (Davis & Shaw, 2001; Thomas *et al*., 2001), as well as coexistence following translocation or reintroduction for conservation (Kleiman, 1989). Predator-naïve animals often fall prey to resident predators (Beck *et al*., 1991; Short *et al*., 1992; Miller *et al*., 1994), and newly introduced predators may behave in ways to which resident prey are not accustomed (Short *et al*., 2002). In both situations, knowledge of antipredator behaviour is important for management. If prey are naïve, pre-release training may be useful to prepare animals prior to reintroduction (Griffin, Blumstein & Evans, 2000). In contrast, if novel predators are the problem, predator control may be the only option (e.g. Morris *et al*., 1998). Moreover, understanding antipredator abilities may also help shed light on historical extinctions. The loss of antipredator behaviour on islands is implicated in vulnerability of insular fauna to extinction (Diamond, 1989; McKinney, 1997). Comparisons between extant and extinct species may identify those behavioural traits responsible for persistence.

In this study, we examined antipredator behaviour to identify likely factors that differ between pademelons and tammars and which may explain the persistence of one and the extinction of the other. Antipredator behaviour includes a variety of traits that function to reduce the likelihood of an individual being killed (Lima & Dill, 1990). We focused specifically on visual and acoustic predator recognition and on group-size effects (Bednekoff & Lima, 1998) – the widespread observation that individuals forage more and allocate less time to antipredator vigilance when around others – and compare our study of red-necked pademelons with the results from previous studies of tammar wallabies (Blumstein, Evans & Daniel, 1999; Blumstein *et al*., 2000). We chose these behaviours because animals must recognize prey to escape, and because by reducing vigilance when aggregated, animals may in fact 'let down their guard' and become more vulnerable to certain predators.

METHODS

Subjects and husbandry

All studies were conducted with adult captive-bred pademelons at the Macquarie University Fauna Park, Sydney, Australia. Subjects had been in captivity for at least one generation where they were protected from exposure to both foxes and cats. Raptors occasionally flew over the animal enclosures. When not participating in the following experiments, subjects lived in mixed-sex aggregations and had access to *ad libitum* kangaroo pellets (Gordon's Stock Feed), natural vegetation and water.

Each subject was fitted with a cat collar 1 cm wide with a 2.2 × 5.0 cm coloured plastic key-chain attached. Uniquely coloured key-chains permitted individual identification. Collars have no adverse effects on animals and have been used to identify individuals in other studies (e.g. Ord,, Evans & Cooper, 1999; Blumstein *et al*., 1999; Blumstein, Daniel & Evans, 2001*b*). Subjects habituated quickly to the collars, and we could detect no sign of external chafing or irritation.

Experiment 1: predator recognition

We selected 18 pademelons (nine males and nine females – three of which had pouch young) for this experiment. Each subject was individually housed in one of three 4 × 9 m 'testing arenas'. The arenas had two 'stages' onto which taxidermically mounted animals could appear, and an observation area where an observer could sit and video-record the focal subject (see Griffin, Evans & Blumstein, 2001 for a plan view). For these experiments, we modified the yards by fencing off the corners farthest from the observer. By doing so, we ensured the animals could always see the presentation stage. Subjects were trained to forage in a central location of the arena while being observed. A single investigator entered the yard and placed a large handful of grated carrots and crushed kangaroo pellets in a central location before leaving the yard and sitting in the experimental 'hide' for 10–30 minutes. This was repeated twice each day (early morning and late afternoon) for the 4 or 5 days it took for animals to forage quietly on the food while being observed. The central location ensured that the subject would be optimally positioned to see any stimulus presented on the stages.

Many species, including nocturnal and crepuscular ones, identify predators visually (e.g. Curio, 1993; Evans, Macedonia & Marler, 1993; Blumstein *et al*., 2000). On six successive mornings, each pademelon was exposed to one of six visual stimuli (see Blumstein *et al.*, 2000 for a photograph of the stimuli). A model thylacine, constructed of injection-molded foam, represented an evolutionarily important, but now extinct, predator. Taxidermic mounts of a cat and a fox represented recently introduced predators. A taxidermically mounted tammar wallaby allowed us to measure the response to a non-predator (pademelons were housed in enclosures adjacent to tammars). In addition, the cart on which all stimuli were presented was a treatment which allowed us to measure the response to the presentation device without a vertebrate stimulus, and a 'blank' trial, in which no stimulus was presented, allowed us to measure spontaneous change in behaviour over time.

Although predators may be silent while hunting, many prey species respond to the sounds of their predators or to predator-related sounds (e.g. Hauser & Wrangham, 1990; Noë & Bshary, 1997; Berger, 1998; Swaisgood, Rowe & Owings, 1999; Berger, Swenson & Persson, 2001). On five successive afternoons, pademelons were exposed to each of five acoustic stimuli which were digitally played back using a PowerBook 100 computer through a Sony SRS-77G powered speaker (see Blumstein *et al.*, 2000 for more details of recording and playback and spectrograms of the stimuli). Each subject was exposed to one of two exemplars for each acoustic treatment broadcast at realistic amplitudes. Treatments included: the sound of wallaby foot-thumps (76 dB), chosen to measure the response to a macropodid acoustic antipredator signal; the calls of a wedge-tailed eagle (90 dB), chosen to document the response to an extant predator with which pademelons evolved; and the howls recorded from a pack of dingoes (92 dB), chosen to represent the sound of an evolutionarily recent predator. Controls included the song of an Australian magpie (89 dB), chosen because it may sing from the ground and is not a pademelon predator, and, once again, a 'blank' trial to allow us to measure spontaneous change in behaviour.

Both visual and acoustic stimuli were presented in a within-subjects, repeated-measures design, in which each subject was exposed to each stimulus once in a predetermined random order. Across treatments, order was balanced so as to control for experiment-wide order effects. Each day, the enclosures were tested in a random order and the side on which the visual stimulus appeared (or on which the speaker was hidden) was alternated between days.

All stimulus presentations were video-recorded and a single observer estimated the time allocated to common behaviours from the videotapes. Behaviours were logged using the event recorder The Observer 3.0 (Noldus Information Technologies, 1995), and analyzed using custom-written analysis algorithms. Following protocols developed in other studies (Blumstein *et al.*, 2000), we used the minute before stimulus presentation to provide a baseline estimate of time allocation, and report the difference between the minute before stimulus presentation and each of 15-second intervals after stimulus presentation as a measure of response to stimulus presentation (see also Blumstein *et al.*, 2000; Griffin *et al.*, 2001).

Responses to both the visual and acoustic stimuli were relatively transient so we focused on only the minute during which stimuli were presented. For visual treatments, we excluded the first 15-second time interval because all stimuli elicited a brief orienting response. Within-subjects repeated-measures ANOVA models were fitted using SuperAnova 1.1 (Abacus Concepts, 1991); we report the Huynh–Feldt corrected *P*-values.

Experiment 2: group size effects

We elected to study group size effects in captivity to control for a number of potential confounding and obscuring variables (Elgar, 1989; Blumstein *et al.*, 1999). We selected ten different adult female pademelons (five with and five without pouch young) for this experiment. We focused on females to avoid the possible confounding factor of having males in a group, as well as to reduce the likelihood of aggressive encounters between males (agonistic behaviour in females was rare and consisted mainly of simple displacements). For this study, we moved subjects temporarily into a 10 × 24 m fenced enclosure which was encased with a band of 90% shade-cloth 2 m tall, to isolate them visually from tammar wallabies in three adjacent enclosures. Animals noticeably 'relaxed' within 1 day of being introduced to the experimental enclosure; they stopped exploring the perimeter of the enclosure, began to groom, and behaved similarly to individuals in other enclosures. Subjects were provided with *ad libitum* kangaroo pellets, access to natural vegetation, and water 24 hours/day. The experimental enclosure contained both natural shade (tree shadows and a patch of dense brush) and artificial cover (concrete tubes). Cover was designed to provide protection against the elements and arranged to facilitate observation and it was constant for all treatments.

By design, we observed: four subjects alone; two replicates of two different pairs of subjects; and single replicates of animals housed in groups of four, six, eight, and ten. Group sizes were ordered so as to minimize the trapping and movement of subjects (for ethical reasons) while also controlling for order effects. The order of group size treatments was: 1, 6, 10, 8, 4, 2, 1, 1, 2, 1.

Subjects were given 2.5 days to habituate to their new surroundings before beginning 10 hours of quantitative observations spread over 2 days. Red-necked pademelons are predominantly nocturnal (Johnson, 1977), but the periods after sunrise and before sunset are active times where the full repertoire of behaviour can be observed. We thus observed pademelons both in the early morning (from sunrise to 2.5 hours after sunrise) and in the early evening (2.5 hours before it became too dark to identify subjects). All observations were conducted from a centrally located hide (constructed against one wall of the experimental enclosure) directly opposite the feeder.

We estimated the time each subject allocated to vigilance, foraging, locomotion, affiliative social behaviour and aggression. Time allocation for the common behaviours (vigilance and foraging) was quantified by noting the activity of the focal subject every 5 minutes during the 10 hours of observation. The rate of the remaining rare social behaviours was estimated by noting each occurrence.

Analyses first focused on three individuals that were present in all group size treatments. The percentage time allocation of each of these individuals was averaged for each group size. Analyses also used each group size treatment as the unit of analysis. For this set of analyses, all individual time allocations were averaged for each group size. We used these averages as the best estimate of time allocation at a given group size, and we fitted linear and non-linear (logarithmic) regression models (using Statview 5.0 – SAS Institute, 1998) to explain variation in the percentage time allocated to foraging, looking, locomotion, and affiliative and aggressive behaviour as a function of group size. An alpha level of 0.05 was used throughout. We report adjusted R^2 values as a measure of goodness of fit.

RESULTS

Experiment 1: predator recognition

Pademelons responded to the visual stimuli (Fig. 1) by increasing time allocated to vigilance ($P = 0.033$) and reducing time allocated to foraging ($P = 0.021$); time allocated to locomotion was not affected ($P = 0.298$). There were no significant interactions between stimulus and time (vigilance $P = 0.807$; foraging $P = 0.958$; locomotion $P = 0.567$). Planned comparisons revealed that presentation of the fox inhibited foraging relative to the blank ($P = 0.004$), the wallaby ($P = 0.030$) and the cat ($P = 0.006$). Presentation of the fox also significantly enhanced vigilance compared to the blank ($P = 0.003$, the wallaby ($P = 0.032$) and the cat ($P = 0.011$). The thylacine inhibited foraging relative to the blank ($P = 0.027$) and the cat ($P = 0.042$), but enhanced vigilance only compared to the blank ($P = 0.045$).

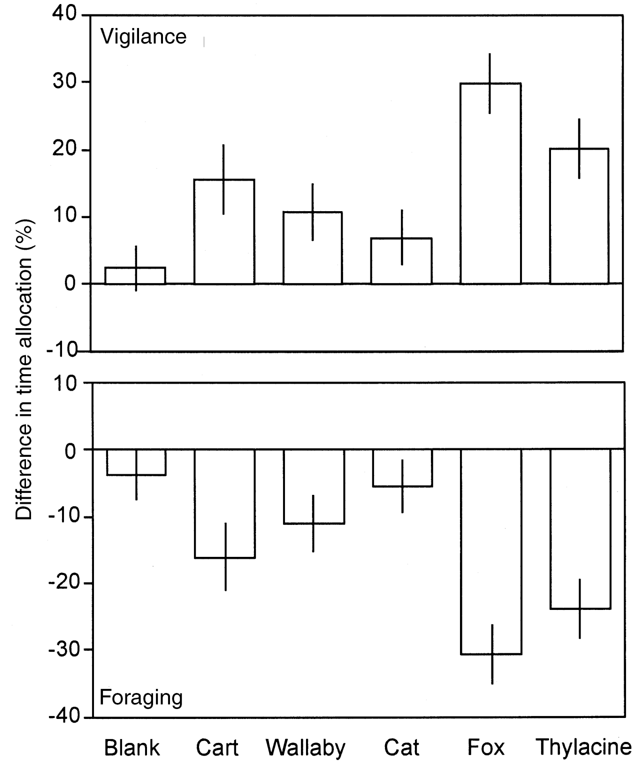

Fig. 1. Percentage difference ($\bar{X} \pm SE$) in the time red-necked pademelons allocated to vigilance and foraging in the final 45 sec of a 60-sec visual stimulus presentation compared to baseline

Pademelons foraged less and were more vigilant in response to all acoustic stimuli (Fig. 2) in the first 15 seconds following playback (foraging $P = 0.0001$; vigilance $P = 0.0001$), but there was no significant effect of playback on locomotion ($P = 0.396$). Planned comparisons revealed that all treatments were significantly different from the blank (foraging largest P-value < 0.005, vigilance largest P-value < 0.001), and that, with the exception of the eagle and the thumps (foraging $P = 0.014$), there were no differences between treatments (foraging smallest P-value $= 0.088$ for magpie/thumps, vigilance smallest P-value $= 0.077$ for thumps/eagle). When analyses of responses to acoustic signals was extended to the entire minute following playback, we found significant effects of playback on foraging ($P = 0.016$), but not on either vigilance ($P = 0.060$) or locomotion ($P = 0.258$). Planned comparisons revealed that the sounds of dingoes ($P = 0.016$), eagles ($P = 0.004$) and magpies ($P = 0.032$) suppressed foraging over the 1-minute period compared to the sounds of thumps, and that the sound of the eagle suppressed foraging compared to the blank. There was, however, a significant interaction between treatment and time for both foraging ($P = 0.0001$) and vigilance ($P = 0.0001$). Pairwise analyses revealed that this interaction was explained by all sounds being significantly different from the blank (all P-values < 0.001), and none being significantly different from each other (all P-values > 0.09). Together, these results suggest a non-specific response to all sounds.

Experiment 2: group size effects

When the behaviour of all individuals in a given group size treatment was averaged, pademelons spent 79% of their time vigilant, foraged for 8.3% of their time, and allocated 5.2% of time to locomotion. They engaged in 0.22 bouts of affiliative behaviour/hour and 0.11 bouts of aggressive behaviour/hour. Focusing on only the three subjects observed at all group sizes revealed similar values (78% time allocated to vigilance, 9.1% time allocated to foraging, and 4.5% time allocated to locomotion – because of their rarity, we did not calculate rates of affiliative or aggressive behaviour in an analogous way).

We could not detect a relationship between pademelon time allocation and group size in any of our analyses

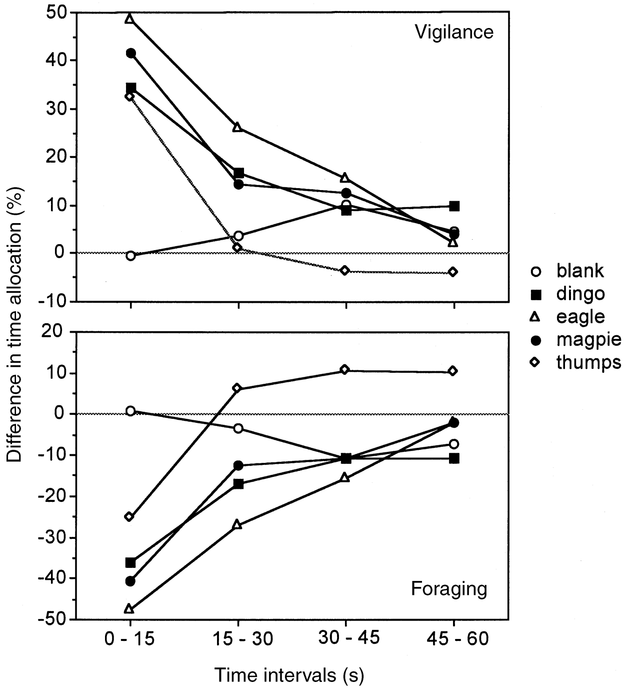

Fig. 2. Average percentage difference in time allocated to vigilance and foraging in each 15-sec time interval following the onset of the acoustic stimulus playback compared to baseline

(Table 1). No significant variation in time allocation was explained by linear or logarithmic regression models. This was true both for the analyses that took the group size treatment as the unit of analysis, and for the more conservative analyses that focused only on the three individuals observed at each of the group sizes. There was a non-significant trend for animals to move around more when in larger groups.

DISCUSSION

We found that red-necked pademelons responded selectively to the sight of some predators, but not to their sounds, nor to a predator-related signal (foot-thumps). After seeing an evolutionarily recent predator (the fox) and an historically important predator (the thylacine), pademelons suppressed foraging and increased vigilance compared to control stimuli. Because our subjects were predator-naïve, we infer some degree of innate predator recognition, such as that which has been described in a variety of other taxa (e.g. insects – Roeder, 1962; amphibians – Ewert, 1980; fish – Magurran, 1986; mammals – Coss, 1999; birds – Curio, 1975).

In contrast, tammar wallabies from Kangaroo Island showed selective recognition of the fox and cat, but not the thylacine (Blumstein *et al.*, 2000). Pademelons may have retained specific responses to the thylacine, and recent evolutionary experience with foxes could have selected for fox recognition. Compared to the Kangaroo Island tammars, which have been isolated from thylacines for 9500 years (Blumstein *et al.*, 2000), mainland pademelons should have more recent evolutionary experience with the thylacine, which was probably driven extinct in the last 3500 years by the introduction dingoes to Australia (Flannery, 1994). Alternatively, pademelons could rely on a less specific predator recognition template. The model thylacine and mounted fox were the largest two stimuli, so it is possible that pademelons used apparent size of stimulus to assess predation risk (e.g. Evans *et al.*, 1993). Additional experiments would be required to identify the specific subset of visual cues that mediate antipredator responses. At this point, it is impossible to differentiate between the above two hypotheses.

Pademelons did not respond differentially to the sounds of predators versus non-predator controls. However, rather than being generally unresponsive, pademelons reacted to all sounds. Previous playback experiments have demonstrated that foot-thumps function as an antipredator signal in tammars (Blumstein *et al.*, 2000). In contrast, pademelons had the most transient responses to foot-thumps, suggesting that they were not assessed as alarming. From these observations, we infer that pademelons are generally responsive to sounds, but did not distinguish among them. Unlike tammars, whose assessment of predation risk is modified by conspecific foot-thumps, pademelons seem to assess risk independently of others.

Unlike most other studied macropodids (Jarman, 1987; Coulson, 1999, Blumstein *et al.*, 2001*b*; Blumstein, Daniel & McLean, 2001*c*; Blumstein & Daniel, 2002; but see Colagross & Cockburn, 1993; Johnson, 1989), including tammars studied under identical captive conditions (Blumstein *et al.*, 1999), red-necked pademelons did not modify their time allocation as a function of the number of nearby conspecifics – they did not have group size effects. This observation is consistent with the hypothesis that despite foraging in

Table 1. Variation (Adjusted R^2) in percentage time allocated to different behaviours explained by group size manipulations in red-necked pademelons. Time allocated to foraging, vigilance and locomotion was estimated by scan samples, while time allocated to the rare affiliative and aggressive behaviours was estimated by all-occurrence sampling. Time budgets were calculated in two ways: by averaging each individual's time allocation at each of six group sizes (n = 1, 2, 4, 6, 8, 10) – 'overall group average'; and by averaging only those three subjects that were present in all six group size manipulations – 'average of three subjects'. Linear and logarithmic regressions were fitted to these data

	Foraging	Vigilance	Locomotion	Affiliative	Aggressive
			Overall group average		
Linear	Adj. R^2 = 0 P = 0.42	Adj. R^2 = 0 P = 0.61	Adj. R^2 = 0.47 P = 0.08	Adj. R^2 = 0 P = 0.64	Adj. R^2 = 0 P = 0.45
Logarithmic	Adj. R^2 = 0 P = 0.40	Adj. R^2 = 0 P = 0.62	Adj. R^2 = 0.55 P = 0.06	Adj. R^2 = 0 P = 0.79	Adj. R^2 = 0 P = 0.41
			Average of three subjects		
Linear	Adj. R^2 = 0.02 P = 0.36	Adj. R^2 = 0 P = 0.61	Adj. R^2 = 0.27 P = 0.17		
Logarithmic	Adj. R^2 = 0.05 P = 0.33	Adj. R^2 = 0 P = 0.61	Adj. R^2 = 0.25 P = 0.18		

aggregations, pademelons independently assess and manage predation risk, rather than becoming less vigilant as the probability of predation decreases with increasing group size.

We suggest that these two traits – remaining relatively less discriminating, and independently assessing predation risk – have helped red-necked pademelons survive the introduction of foxes to the Australian mainland. Interestingly, the Tasmanian pademelon (*Thylogale billardierii*) used to live on mainland Australia, but now only survives on Tasmania and some Bass Strait islands (Watts, 1993; Johnson & Rose, 1995). If our hypothesis is correct, Tasmanian pademelons might be expected to behave more like tammar wallabies than the congeneric red-necked pademelon.

There are other behaviours that seem to differ between the species. Observations of all three species in the field suggest that when alarmed on foraging grounds, red-necked pademelons hop low and quickly through the dense cover. Tasmanian pademelons, like tammar wallabies, hold their body in a more upright posture when fleeing. Such differences in posture may influence maximum escape speed, or agility, and therefore could be important in explaining persistence on the predator-rich mainland.

Only by understanding why species are threatened can we hope to moderate our current extinction event. A fundamental understanding of antipredator behaviour is important whenever predation is a potential cause of endangerment (Curio, 1996; Anthony & Blumstein, 2000; Berger *et al.*, 2001; Blumstein, Daniel & Bryant, 2001*a*). In this case, red-necked pademelons seem to have a relatively independent, but sufficient, predator recognition strategy, while tammars appear to rely more on their conspecifics for assessing and managing predation risk. This result begs the more general question about whether social species are more vulnerable than less social ones to predation and/or extinction. Such an issue is best studied with comparative techniques (Harvey & Pagel, 1991).

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