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Selective Learning in a Marsupial

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Abstract

Behavioural plasticity allows animals to adjust rapidly to local environmental conditions, but at the risk of erroneously changing behaviour in response to irrelevant events. Adaptive biases or predispositions constrain learning and reduce such potential costs. Preferential learning about complex biologically-meaningful stimuli, such as predators, has been investigated in only a few systems and there have been no experimental tests for the presence of adaptive biases in a marsupial. We have previously shown that tammar wallabies (*Macropus eugenii*) became fearful of a model fox (*Vulpes vulpes*) after it was repeatedly paired with an aversive event. Tammars generalized their acquired response to a cat (*Felis catus*), but not to a non-predator (juvenile goat, *Capra hircus*), suggesting that they might have a bias to associate predators with frightening events. The present study tested this idea directly. We used an experimental design identical to that of earlier predator-training experiments, but substituted a model goat for the fox as the stimulus predicting a capture attempt. A control group had the same total experience of the goat and of a human with a net, but without any predictive relationship between these two events. We detected no change in behaviour towards the goat, or to any of an array of control stimuli, as a consequence of training. This finding contrasts strongly with the effects of the same pairing procedure using a fox model. Taken together, these studies provide the first evidence for an adaptive predisposition to acquire a fear of predators in marsupials. Learning processes in this group are thus evolutionarily convergent with those previously described in eutherian mammals.

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Introduction

It was once thought that animals could learn about all events with equal ease (Pavlov 1927). There is now, however, increasing evidence that they may learn selectively about only a subset of the experiences that impinge upon them. Studies of learning in ecologically-relevant contexts have identified biases that increase the probability that animals will learn about complex functionally-critical stimuli, such as the appearance of a predator (Curio 1988; Mineka and Cook 1988; Magurran 1989), features of their mother (Bateson 1991; ten Cate 1994) or their natal song (Marler 1997). The term 'guided learning' acknowledges the adaptive nature of such phenomena (Gould and Marler 1987).

In both song learning and imprinting, there is evidence that the propensity to learn preferentially about some stimuli rather than others is mediated by differences in salience. For example, 48-h-old domestic chicks reared in darkness nevertheless show a strong spontaneous preference for stimuli containing head and neck features (Johnson and Horn 1988; Johnson and Morton 1991). The naive response to such cues produces imprinting on hen-like objects by ensuring that chicks attend to and approach these stimuli soon after emergence; they are consequently associated with reinforcing events, such as parental care (Johnson and Morton 1991; Bolhuis 1999). Similarly, some song structures are inherently salient and serve as cues that guide song learning in male oscines (Marler and Peters 1988; Soha and Marler 2000).

It is less clear whether selective learning in the context of acquired predator recognition is mediated by differences in initial stimulus salience. Predator-naive European minnows (*Phoxinus phoxinus*) have similar responses to the odour of a northern pike (*Esox lucius*) and that of a non-predator fish, but they acquire a significantly greater fear response to the odour of the predator when it is paired with fish alarm substance (Magurran 1989). Similarly, juvenile rhesus macaques (*Macaca mulatta*) have the same initial response to a toy snake as to a control stimulus (a bunch of flowers), but after identical presentations of these stimuli in conjunction with video footage of a fearful conspecific they learn to associate fear only with the snake (Mineka and Cook 1988). In contrast, the initial presentation of a model Australian honeyeater (*Philemon corniculatus*) elicits a greater response from blackbirds (*Turdus merula*) than a plastic bottle, and when each of these stimuli is paired with the experience of a conspecific apparently mobbing them, the magnitude of the acquired antipredator response to the honeyeater is much greater (Curio et al. 1978).

Guided learning is a particularly exciting area of research because it puts the study of animal learning into an explicitly evolutionary and functional framework. Surprisingly, few studies have investigated this phenomenon in eutherian mammals (Mineka and Cook 1988), and none has examined whether marsupials display guided learning. Given the evidence for learning biases in birds and fish, marsupials represent an excellent opportunity to investigate the possibility that similar ecological pressures may have selected for convergent learning properties in phylogenetically-distant groups.

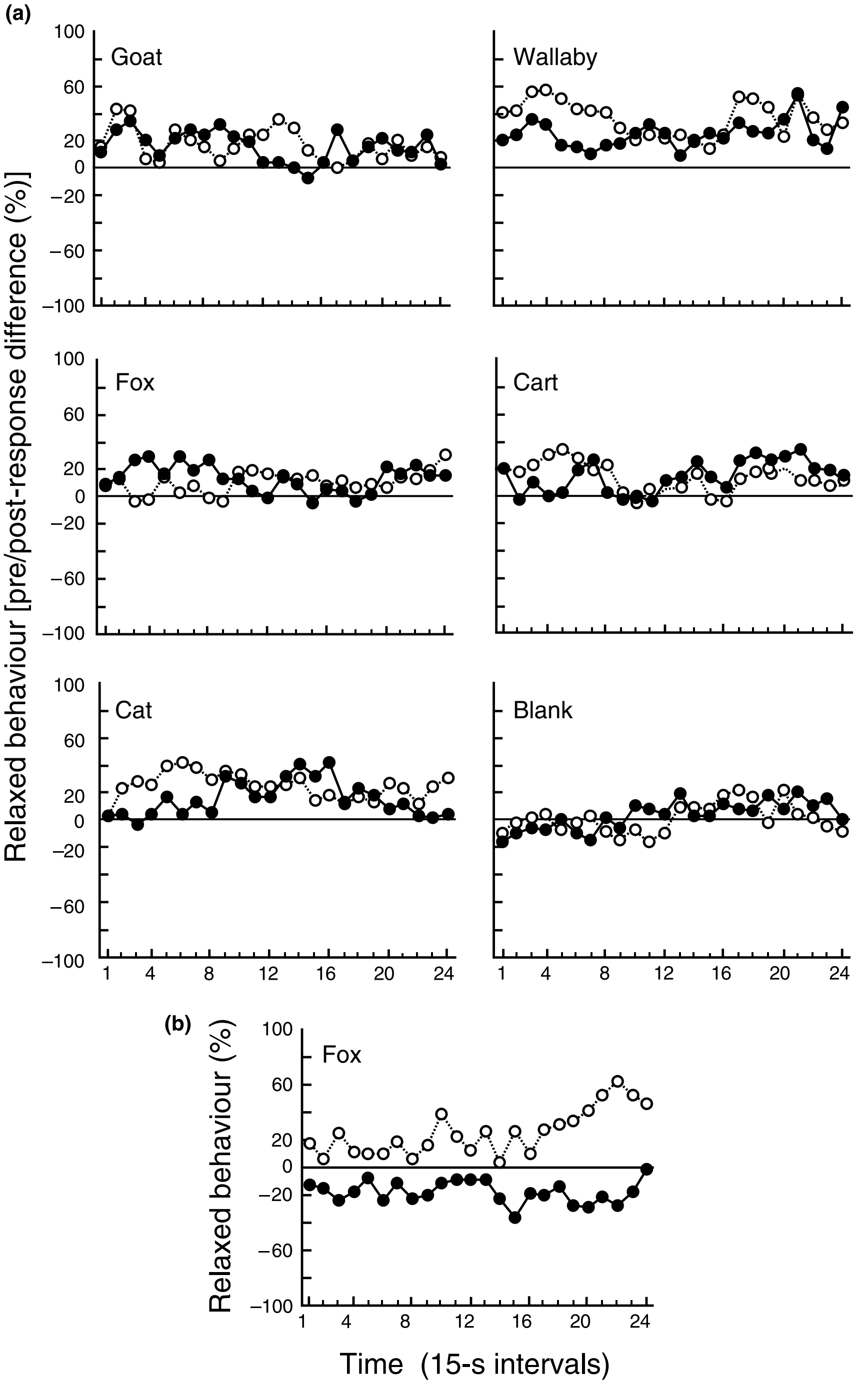
We have recently shown that the responses of tammar wallabies (*Macropus eugenii*), a native Australian marsupial, to a taxidermically-prepared fox (*Vulpes vulpes*) can be enhanced by presenting this novel stimulus in conjunction with an aversive event [a human simulating a capture procedure (Griffin et al. 2001)]. We tested wallabies with an array of other unfamiliar stimuli to determine the specificity of this change in behaviour. Training with a fox produced increased responses to another model predator (cat, *Felis catus*), but not to a size-matched non-predator (juvenile goat, *Capra hircus*), or other controls such as the presentation device. These results suggest that tammars may not acquire fear response to any stimulus that is associated with an aversive event, but rather might be predisposed to learn quite specifically about predators.

In the present study, we addressed this question directly by attempting to inculcate a fear response to a taxidermically-prepared non-predator (juvenile goat), using exactly the same procedure as in our previous study (Griffin et al. 2001). Humans with nets reliably evoke alarm responses, including fleeing and foot thumping (Griffin et al. 2001). We used simulated capture attempts as a standard fear-evoking stimulus so that we could conduct a controlled study of the properties of learning. To determine whether training with the model goat changed the animals' responses to other visual stimuli, we also measured responses to an array of visual models, both before and after training (pre-/post-training trials). Our design incorporated a control group in which animals were exposed to all of the same stimuli as those that were being trained, but with no predictive relationship between goat and human. Comparisons between the responses of these two groups allowed us to detect changes in behaviour attributable specifically to learning. Finally, to determine whether selective learning was mediated by differences in the inherent salience of the goat and fox models, we compared the spontaneous (i.e. pre-training) responses evoked by each of these stimuli.

Methods

Subjects and Husbandry

We randomly selected 16 adult tammar wallabies (eight females and eight males). Animals were temporarily removed from large breeding groups in the Macquarie University Fauna Park and returned to these at the end of testing. To our knowledge, none of these animals had ever had any contact with goats or foxes. In contrast, cats are seen occasionally within the Fauna Park. Subjects were all bred from the same original wild-caught stock. Today, however, tammars only survive on predator-free off-shore Australian islands, but they evolved with a range of now-extinct marsupial predators, such as the Thylacine (*Thylacinus cynocephalus*) (Jones and Stoddard 1998). Foxes and cats are likely to share convergent vertebrate morphological features (e.g. frontally placed eyes; Griffin et al. 2001) with such historically-important predators, but tammars have no evolutionary experience with these introduced species, or with goats.


(a)
Goat
Wallaby
Fox
Cart
Cat
Blank
Relaxed behaviour [pre/post-response difference (%)]
100
60
20
0
−20
−60
−100
1
4
8
12
16
20
24
(b)
Fox
Relaxed behaviour (%)
Time (15-s intervals)

Individual Test Enclosures

Housing and testing conditions have been previously described (see Fig. 1 in Griffin et al. 2001). Briefly, each wallaby was held in a small (length 12 m × width 4 m) individual enclosure. The fence was fully screened except for a 1 × 0.4 m opening which allowed the observer to watch and videorecord the animal, and two 1.5 × 1 m openings (stages), in which visual stimuli were presented. Stimuli were fixed to a cart that ran on inclined rails and could be pulled quietly onto and off the stages by means of a string and pulley system.

Experimental Protocol

Acclimatization

We first habituated each wallaby to foraging while an experimenter was present in the hide by placing a small pile of preferred food (rolled oats) in the centre of the pen (Griffin et al. 2001). Most animals learnt to forage while being observed within 3 d ($\bar{x} = 3.06$ d, range = 2–5 d). Behavioural testing began once the animal had come to feed on two consecutive occasions.

Experiments

Experimental design was identical to that used in a previous study in which we successfully enhanced the responses of tammar wallabies to a model fox (Griffin et al. 2001). We used the same methods for two reasons. First, the results from the previous study demonstrated clearly that these techniques were an effective way of studying the properties of learning in tammar wallabies. Secondly, by changing the training model from a predator to a non-predator, but holding all other factors constant, we could determine whether tammars learn preferentially about a model fox. Development of these techniques has been described previously (Griffin et al. 2001).

Each wallaby first received six pre-training trials during which we measured its initial response to an array of stimuli, presented in a random order. We then conducted four training trials in which a model goat was either paired (experimental group, see below) or explicitly-unpaired (control group, see below) with a simulated capture procedure. After training, each animal underwent six post-training trials in which it was shown the same set of stimuli as in the pre-training trials, but in a different random order. Throughout the study, the

Fig. 1: (a) Changes in relaxed behaviour following training with a model goat (non-predator) for the paired-experimental (—●—) and unpaired-control (····○····) groups. The mean pre/post-response difference is plotted for 24 time intervals (15 s) from stimulus onset, 1 min during stimulus presentation and 5 min after the stimulus had disappeared from the stage. Note that enhanced responses to the non-predator will be reflected in a reduced proportion of relaxed behaviour (see text for details). (b) Changes in relaxed behaviour (pre/post-response difference) following training with a model fox (predator) for the paired-experimental (—●—) and unpaired-control (····○····) groups (redrawn from Griffin et al. 2001)

stage on which the stimulus appeared was alternated from trial to trial to reduce the likelihood of habituation.

Pre- and post-training trials

We used the same array of stimuli as in our earlier fox-training study (Griffin et al. 2001). Vertebrate models were taxidermically-prepared mounts. A juvenile goat represented a non-predator and was also the model with which the animals were trained. Fox and cat models allowed us to test whether training with the goat led to increased responses to these representative predators, which appear to be inherently more aversive to tammars than control stimuli (Blumstein et al. 2000). Finally, we showed the animals a model wallaby to determine the effects of presenting a vertebrate stimulus that was neither novel, nor a predator. Responses to the four vertebrates were compared with those evoked by two control stimuli. The cart was presented alone to measure the response to the presentation device and its associated movement in the absence of a vertebrate stimulus, and blank trials (in which no stimulus was presented) were conducted to measure general changes in behaviour associated with training.

Training trials

For training, animals were randomly assigned to a paired (experimental) or an explicitly-unpaired (control) group. The paired group underwent training trials in which the juvenile goat appeared on the stage approx. 3–5 s before a human carrying a net emerged through the hide opening and began a simulated capture attempt. In this group, the appearance of the goat thus reliably predicted an aversive event. Animals were run four times back and forth in the enclosure along the fence, while the net was held just above the ground, but they were never caught. The human then exited the yard through the hide opening and the goat was withdrawn from the stage approx. 2 s later. The whole procedure lasted approx. 60 s.

The unpaired-control group also underwent four simulated capture procedures and was presented with the goat four times, for 60 s each, but these two events were never simultaneous. Instead, they were separated by a minimum of 25 min and a maximum of 90 min. In half of the trials, the animals saw the goat first and in the other half they experienced the simulated capture first. For this group, there was thus no predictive relationship between goat and aversive event.

Note that the overall experience of wallabies in the paired and the unpaired groups was identical in all respects (i.e. exposure to the goat stimulus and simulated capture attempts was matched), except for the goat–human contingency, which was experienced by the paired group only. We conducted planned comparisons between the paired and the unpaired groups using response change in the presence of the goat between pre- and post-testing. This allowed us to detect changes specifically attributable to learning (Shettleworth 1998) and to separate such effects from those that might be a consequence of other factors, such as confinement in the test yards and repeated exposure to the non-predator model.

Test procedure

Testing procedures have been described previously (Griffin et al. 2001). Briefly, a single stimulus was presented for 60 s on the stage during each pre- and post-training trial. Stimuli were presented only if the subject was foraging at the centre of the pen or engaged in other relaxed behaviour such as grooming or sitting. This procedure controlled both baseline behaviour and the location of the animals when they first saw the visual stimuli. Upon completion of the post-training trials, all subjects were returned to their social groups.

Data Analysis

Data were analysed in the same way as in our fox-training study (Griffin et al. 2001). We videorecorded wallabies for 1 min immediately prior to stimulus presentation (baseline), 1 min during the stimulus presentation and 5 min after the stimulus had disappeared from the stage. Behaviours were grouped into three categories: vigilance (bipedal stand), relaxed (forage, sit with tail between legs, groom) and locomotion (hop, pentapedal walk). We scored behaviour from video recordings using The Observer 3.0 (Noldus Information Technologies 1995), which provided a timing resolution of 0.1 s.

To assess responses to each stimulus, we measured changes in behaviour over time. We focus particularly on changes in relaxed behaviour and report these only. Reductions in relaxed behaviour reflect all transitions to an alarmed state, which is typically characterized by alternating bouts of vigilance and locomotion. Both of these behaviours are adaptive if faced with a predator. Relaxed behaviour thus provides an aggregate measure that is a particularly sensitive assay for assessing overall antipredator response.

The percentage of time spent in each behaviour was determined for the 60-s baseline and for 24 successive 15-s intervals after stimulus onset. We then calculated difference scores for each 15-s interval, relative to the pre-stimulus baseline. To quantify the effects of training, we calculated the change in percentage of time spent in each behaviour between pre- and post-training trials (pre/post-response difference) for each stimulus, group and 15-s time interval. We then compared the paired group's mean pre-/post-response difference to that of the unpaired group using a two-way repeated measures ANOVA with factors for group (paired/unpaired) and time (successive 15-s intervals). To test for differences in the inherent salience of the goat and the fox, we pooled the pre-training responses of the experimental and the control groups to each of these stimuli to increase statistical power ($n = 16$) and then compared them using a two-way repeated measures ANOVA with factors for stimulus and time.

Statistical analyses were carried out using STATVIEW 5.1 (SAS Institute 1998) and SUPERANOVA 1.1 (Abacus Concepts Inc. 1991). As sequential measures of

Table 1: Results of a two-way repeated measures ANOVA (group × time) comparing the mean pre-/post-response difference in relaxed behaviour of the paired-experimental group with that of the unpaired-control group for each stimulus

	ANOVA factor			
	Group main effect		Group × time interaction	
Stimulus	$F_{1,14}$	P	$F_{23,322}$	p^a
Goat	0.004	0.477^b	0.665	0.741
Fox	0.014	0.908	0.634	0.758
Cat	0.220	0.646	1.190	0.295
Wallaby	0.556	0.468	0.675	0.740
Cart	0.002	0.966	0.706	0.674
Blank	0.029	0.867	0.774	0.661

[a] Huyn and Feldt (1976) corrected (see text).
[b] One-tailed comparisons; all others are two-tailed.

behaviour are typically more highly correlated than more temporally-distant ones, we report Huyn and Feldt (1976) adjusted p-values for all analyses involving a time factor. Comparisons involving responses to the goat in the paired-experimental vs. unpaired-control group for which we had a priori predictions were one-tailed; all others were two-tailed. We used an α of 0.05 throughout.

Results

Following training, animals for which the goat had predicted the onset of a capture procedure showed no changes in any of the behavioural responses measured as a consequence of this experience. Statistical comparisons between the paired-experimental and the unpaired-control groups also revealed no differences in relaxed behaviour in response to any of the other vertebrate models, or to the control stimuli, following training with the goat (Fig. 1a, Table 1). Similar results were found when analysing changes in vigilance and locomotion (Griffin 2001). This pattern of results contrasts strongly with those obtained in a previous study (Fig. 1b) in which the same contingency had inculcated a fear of foxes that generalized to another predator model (Griffin et al. 2001).

To determine whether failure of the wallabies to learn in the present study was attributable to differences in the inherent salience of the fox and the goat, we compared the animals' naive responses to these stimuli. There were no significant differences between the pre-training responses evoked by the fox and those elicited by the goat (vigilance: $F_{1,14} = 0.164$, $p = 0.691$; locomotion: $F_{1,14} = 0.130$, $p = 0.724$; relaxed behaviour: $F_{1,14} = 0.251$, $p = 0.624$), suggesting that these vertebrates did not evoke different levels of antipredator behaviour before training.

To ensure that results would not be affected by previous training experience, we used a different set of subjects in the present study from those tested in the first series of experiments. We compared the pre-training responses evoked by the goat and by the fox in the present study with those that had been elicited by each of these stimuli in the fox-training experiment, to test whether these two groups were systematically different. Wallabies from both studies showed similar initial levels of vigilance ($F_{1,30} = 0.140$, $p = 0.711$), locomotion ($F_{1,30} = 0.290$, $p = 0.594$) and relaxed behaviour ($F_{1,30} = 0.134$, $p = 0.717$) in response to the goat. Naive responses to the fox were also similar (vigilance: $F_{1,30} = 0.243$, $p = 0.626$; locomotion: $F_{1,30} = 0.110$, $p = 0.742$; relaxed behaviour: $F_{1,30} = 0.464$, $p = 0.501$). While the results of such cross-study comparisons should be interpreted with caution, differences in the effects of the experimental contingency do not seem to reflect differences between the two subject populations.

Discussion

Tammars failed to acquire a fear response to the model goat. We could detect no changes in the behaviour evoked by this stimulus in the experimental group, relative to control animals that had the same total experience of the goat and the human, but with no predictive relationship between them (Fig. 1a). This finding is in striking contrast with that of a previous study using identical techniques, which demonstrated that tammar wallabies rapidly learn to associate a model fox with simulated capture attempts and that they behave more cautiously towards this predator stimulus following training (Fig. 1b).

There are several possible explanations for the failure of wallabies to associate a representative non-predator with aversive events. Animals may differ in their ability to learn because they originate from genetically distinct populations (Tulley and Huntingford 1987), have been reared in different conditions (Winterfeld et al. 1998), or have had prior experience with the stimuli with which learning is attempted (Mackintosh 1974, 1983). The first two explanations do not apply here because animals were all captive-bred from the same wild-caught original stock and reared under identical conditions. Prior experience with a stimulus can block learning about it (Mackintosh 1974, 1983), but this also seems unlikely. We deliberately selected a new set of naive subjects for the present study to exclude the possibility that tammars might fail to acquire a fear response to the goat because of prior exposure to this model, which had been used as part of a stimulus array in the fox-training experiment (Griffin et al. 2001). To our knowledge, neither group of wallabies had ever seen live foxes or goats.

Comparisons with earlier experiments show that wallabies in the present study did not respond differently to the goat before training than those that had previously acquired antipredator responses to a fox using the same procedure (Griffin et al. 2001). There were also no differences in the naive responses of the two groups to the fox. These findings should be interpreted with caution because of potential confounding factors such as time of year. However, we have documented the responses of tammar wallabies to model predators in the course of several studies and have not found any seasonal effects (D. T. Blumstein & A. S. Griffin, unpubl. data). All other experimental conditions were matched in both experiments. Hence, variation in initial responses to the stimuli with which training was attempted does not appear to account for differences in whether or not learning occurred.

In summary, the failure of wallabies in the present study to learn about a non-predator, whereas those in the previous study acquired a fear response to a predator with an identical training regime, is unlikely to be attributable to differences between the two groups in genetic origin, rearing conditions, or prior experience with goats and foxes. We conclude that tammar wallabies are predisposed to selectively associate predators with threatening events.

Biases in learning likely function to enhance the probability that animals will acquire responses to functionally-critical stimuli. This phenomenon may, however, be mediated by a range of mechanisms. First, the stimulus about which animals learn preferentially may be inherently more salient than one about which learning is impaired (Bolhuis 1999). Selective learning would thus be a consequence of selective attention. In the present study, initial responses to the goat did not differ significantly from those evoked by the fox, suggesting that the non-predator was not less salient to the wallabies than the predator. Alternatively, biases in learning may reflect the preferential formation of an association between particular kinds of stimuli, such as those between specific visual cues and fear, or between sounds and fear (Foree and LoLordo 1973). The results obtained in the present study are consistent with a mechanism of this kind. It would hence be predicted that, while non-predators are not readily associated with a fear response, they could become associated with other kinds of events, such as resource availability. Experiments in which the goat was used to predict the presentation of food would allow a test of this hypothesis. Finally, a bias in learning can appear if acquiring information about some kinds of stimuli requires more extensive experience, or more intense reinforcers. In the present study, it is conceivable that tammars might have learnt to fear the goat model if the number of training trials had been increased or if a more frightening aversive event than the simulated capture had been used. Further research will be necessary to determine which of these mechanisms is responsible for guided learning in tammars, although ethical considerations constrain the range of possible manipulations.

To our knowledge, only one previous study has revealed preferential learning about a predatory stimulus in mammals. Mineka and Cook (1988) showed that juvenile rhesus macaques (*M. mulatta*) acquired a fear response to a snake after being shown videorecordings of adults behaving fearfully towards it. In contrast, they did not learn about an equally novel control stimulus (plastic flowers) when this was paired with identical video sequences. The present study provides the first evidence for a similar predisposition to form selective associations in a marsupial. Together with previous demonstrations of guided learning in the context of acquired predator recognition in birds and fish (Curio 1988; Magurran 1989), this result suggests that natural selection has produced convergent cognitive properties in phylogenetically-distinct groups.

The ability to acquire fear responses entails the risk of mistakenly learning about a broad range of innocuous stimuli. Such mistakes are potentially costly. Guided learning may act as a safeguard to ensure that only relevant events cause subsequent changes in behaviour. A predisposition to associate fear specifically with predators reduces the probability that a wallaby startled or frightened by a non-predator, or some other environmental event, would make non-adaptive changes in behaviour as a consequence.

Our results have both theoretical and practical implications. The existence of a learning bias in tammar wallabies suggests that experience may play an important role in predator avoidance by macropod marsupials. This result is encouraging for conservation managers interested in reintroducing captive-bred endangered animals to the wild because the intervention of training animals about predators prior to release may effectively emulate natural processes (Griffin et al. 2000; McLean et al. 2000).

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