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Training Tammar Wallabies (*Macropus eugenii*) to Respond to Predators: A Review Linking Experimental Psychology to Conservation

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Animals bred in captivity often suffer high levels of predation after release into the wild. Prerelease predator avoidance training has been undertaken to try to improve antipredator skills. Applied research on predator avoidance learning in birds and mammals has not benefited from the empirical findings of extensive basic research, as it has been the case for fish. Consequently, this field has progressed slowly and the utility of prerelease antipredator training as a conservation strategy remains controversial. Here, I report one experiment and review two others that illustrate the way in which principles and experimental designs borrowed from classic studies of animal learning can be used to develop predator avoidance training techniques and to establish the content of learning. Results show that tammar wallabies (*Macropus eugenii*), an Australian macropodid marsupial, can acquire a fear response that is specific to predators, but that the likelihood of learning is dependent upon subtle details of the training protocol. Differential reinforcement of predator and non-predator stimuli has the potential to enhance the specificity of learning, if necessary. I discuss the implications of these results for the field of predator avoidance training and suggest that a controlled experimental approach, which enables the content of learning to be described, will be the most fruitful for this research area in the long term.

Species extinction rates have reached all time highs (IUCN, 2000). Reintroduction of animals bred in captivity is a common conservation strategy, but few programs have succeeded in establishing sustainable populations (Beck et al., 1994; Wolf et al., 1996). A widespread difficulty is predation which causes high levels of postrelease mortality (Banks et al., 2002; Brown & Laland, 2001; Dunham, 1997). Prerelease predator avoidance training has consequently been used to try to improve antipredator skills. Training usually involves the simultaneous presentation of the target predator and an unpleasant event (see Griffin et al., 2000).

Predator avoidance learning in fish has been the focus of much basic research (see Brown & Laland, 2001). A controlled experimental approach has led to a good understanding of the properties of learning and its effect on survival in this taxonomic group. In contrast, most studies of predator avoidance learning in birds and mammals have been undertaken within the applied context of antipredator training. Wildlife managers deal typically with species on the brink of extinction and are under pressure to fix problems with only limited time and resources.

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Consequently, there have been few systematic studies of the effects of training on either prerelease or postrelease behavior in these groups (see Griffin et al., 2000; but see Curio, 1993; Mineka & Cook, 1988). Today, the use of predator avoidance training remains controversial because it is not known whether it provides any postrelease survival benefit. While the results from one study suggest that prerelease training enhances survival (Ellis et al., 1977), those from another reveal no effect (Miller et al., 1994). A third finds a beneficial influence if animals are trained with a live predator, but not after training with a model (van Heezik et al., 1999). Even these results, however, are difficult to interpret because none of these studies demonstrated that the animals learnt specifically to fear the target predator during training. I suggest that such postrelease survival tests require first a good understanding of the content of learning. This can be gained by using a more controlled experimental approach to the study of antipredator training.

Over a century of experimental psychology has now firmly established how, what and under which conditions, animals can learn (see Shettleworth, 1998). These questions have been explored traditionally using arbitrary stimuli, such as single tones and lights. Nevertheless, it is likely that learning about biologically significant stimuli, such as predators, will follow the same principles. This body of theoretical and empirical research tells us how animals can be trained to respond fearfully to novel objects. It also describes experimental designs, which demonstrate that changes in behavior are attributable to associative learning and that acquired responses are specifically evoked by the training stimulus. This information can hence be used both to design antipredator training protocols and to explore the effects of such interventions systematically.

On mainland Australia, introduced foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) are strongly implicated in the decline of small and medium-size marsupials (Maxwell et al., 1996). These predators have also been identified as a primary cause of the failure of many reintroductions and translocations (Short et al., 1992). Tammar wallabies (*Macropus eugenii*) are a 3-7 kg macropodid marsupial, which inhabited broad areas of south west and south east Australia until the early 1900s (Smith & Hinds, 1995). Exotic predators, together with hunting by European settlers and habitat destruction, are the principal factors invoked to explain the strong decline of this medium-size kangaroo and its extinction from South Australia. The only substantial populations remaining today are those that survive on fox-free islands, such as Kangaroo Island off the south coast of Australia. This population evolved with a range of marsupial predators, such as the now extinct marsupial tiger (*Thylocinus cynocephalus*), before the island's isolation from the mainland by rising sea levels at the end of the last glaciation, 9500 years ago. Since then, these tammars have not typically been exposed to mammalian predators. While low densities of feral cats and farm dogs inhabit the island, these species are generally restricted to the proximity of human settlements (Blumstein et al., 2000). There are current plans to reintroduce tammar wallabies back to the mainland so there is an urgent need to develop techniques that maximize postrelease survival.

Tammar wallabies have been the focus of a long term research program that aims to understand the properties of predator recognition and predator avoidance learning. The objective of the present paper is to report one experiment and to review two others that were designed to enhance their antipredator responses. I used visual predator stimuli for training, because vision appears to play an important role in the antipredator behavior of this species. Tammars suppress foraging and increase vigilance significantly more in response to the sight of predator models than in response to that of control stimuli (Blumstein et al., 2000). In contrast, there is no evidence for either olfactory (Blumstein et al., 2002) or acoustical predator recognition (Blumstein et al., 2000). Another line of evidence pointing to the importance of vision comes from physiological and anatomical studies of the tammar's visual system. Results reveal that the ventral retina provides for high contrast sensitivity, but low spatial acuity, suggesting that it has become specialized for the detection of aerial predators (Hemmi & Grünert, 1999). While primarily nocturnal, tammars forage in open habitats in the morning and late afternoon (Blumstein et al., 1999), which may be the reason why visual predator recognition evolved.

In the first experiment, I tested the effects of several different training protocols on the animals' responses to a model predator (fox) in order to select the method that inculcated the greatest change in behavior. The second experiment was designed to test whether such changes were attributable to associative learning and whether acquired fear responses were specific to the predator with which the wallabies were trained (Griffin et al., 2001). The third experiment examined whether differential reinforcement of predatory and non-predatory stimuli during training enhanced the specificity of the acquired response (Griffin & Evans, 2003). Subjects were all adults aged between two and five and were either wild-caught from Kangaroo Island or captive-bred descendants of this stock. All had been in captivity for at least two years prior to the experiments. Wallabies were randomly selected for each experiment from large breeding groups at Macquarie University Fauna Park. No subject took part in more than one experiment. To my knowledge these individuals had neither historical (i.e., exposure over evolutionary time), nor ontogenetical (i. e., exposure during individual lifetime), experience with foxes. In contrast, cats are seen occasionally within the fauna park.

Experiment 1: Selecting an Optimal Training Technique

During training, the subject must learn to associate a target predator, which initially evokes no or low responses, with an aversive experience, which elicits a spontaneous fear response. The predator is thus equivalent to a conditioned stimulus (CS), and the aversive stimulus functions as an unconditioned stimulus (US). While it is well established that a variety of training parameters influence the likelihood of associative learning (see Mackintosh, 1974; Schwartz, 1989), these may be unfamiliar to wildlife managers. First, the nature of the US has a major impact. Some USs produce faster learning than others (Rescorla, 1988a). The level of asymptotic acquisition may also increase with the intensity and the salience of the US (Annau & Kamin, 1961; Pavlov, 1927). Training techniques are usually designed to make the target predator aversive by chasing the subjects with it, and to reinforce this experience, by simultaneously broadcasting playbacks of social alarm signals (Hölzer et al., 1996; McLean et al., 1995; McLean et al., 1999; van Heezik et al., 1999). There have also been a few attempts to use live predators in which the aversive USs, namely being chased, growled at, stared at, nuzzled and even hurt, are inherent to the predatory stimulus (Ellis et al., 1977; McLean et al., 2000; van Heezik et al., 1999).

Second, the spatial and temporal relationship between the CS and the US are important determinants of learning. Animals are more likely to learn the associative relationship between a CS and a US if these are presented in close spatial contiguity (Christie, 1996) and if the CS is presented just prior to the onset of the US (Pavlov, 1927). Subjects are also most likely to acquire a response to the CS if this event predicts the onset of the US (Rescorla, 1988b). To my knowledge, no antipredator training study has attempted to exploit a predictive CS-US relationship. In most studies, the CS and US occur simultaneously (Hölzer et al., 1996; Maloney & McLean, 1995; McLean et al., 1996; McLean et al., 2000; Miller et al., 1990). Classic studies of animal learning have shown that simultaneous conditioning is less effective than conditioning in which the CS precedes and overlaps with the US (see Mackintosh, 1974).

Third, conditioning to one CS occurs against a background of other CSs (Rescorla & Wagner, 1972), some of which may also predict the onset of the US. Theoretical and empirical studies consistently show that learning about one CS may reduce or even block learning about others (see Mackintosh, 1974). This occurs because animals tend to learn about the best predictor of the US, rather than about all of them (Kamin, 1969; Rescorla & Wagner, 1972). Acquiring responses to contextual cues other than the predator, such as the experimental environment, is likely to be a major drawback in antipredator training and should be avoided.

Finally, the level of learning may vary with the number of training episodes. Too few trials may not be enough for learning to occur and too many may cause habituation and hence counteract the effects of learning. Under controlled conditions, rats require as few as five training trials to learn an associative relationship between a noise and an electric shock (Kamin et al., 1963). However, the number of training episodes required for learning to occur is likely to be dependent upon the nature of the US (Rescorla, 1988a). Most attempts to train animals to respond to predators involve one or two paired presentations of the CS and US (see Griffin et al., 2000).

To my knowledge, there have been no formal tests of the effects of such experimental variables on the likelihood of predator avoidance learning. I began by selecting an optimal training procedure to enhance the responses of predator-naïve tammar wallabies to a fox. I compared the effects of five different training procedures. The optimal approach would be that which produced the largest, most sustained increase in the wallabies' antipredator responses, while being sufficiently controlled to enable me to describe the content of learning in subsequent studies. I elected to train the wallabies using a realistic model predator (fox) to provide high levels of experimental control. In contrast to other antipredator training studies, I exploited a predictive CS-US relationship by presenting the model just prior to the onset of the aversive US. I examined the way in which the spatial proximity of the US and the CS, as well as the number of training episodes influenced the likelihood of learning. I also investigated whether the presence of a second predictor of the aversive event blocked learning about the fox model. Finally, I tested whether the nature of the US had an effect by pairing the fox with two kinds of aversive events, namely a human mimicking a capture attempt or a playback of a macropod social alarm signal. Approaching humans carrying nets consistently elicit high alarm responses in captivity, involving high speed fleeing and alarm thumping, probably because animals associate them with being caught, bagged and handled, which are common management procedures. Simulated capture was not used to emulate the experience of attack by a real predator, but to provide a standard aversive US that was sufficient to elicit a high-level alarm response. Social alarm signals are effective for triggering learning about predators in some species (Curio et al., 1978; Mineka & Cook, 1988). Earlier playback experiments had demonstrated that tammar wallabies suppress foraging and increase vigilance more in response to the sound of macropod alarm thumps than in response to playbacks of control sounds (Blumstein et al., 2000). This finding raised the possibility that this alarm signal might trigger predator avoidance learning in tammars. To determine the effects of training, I measured each animal's response to the fox both before (pretraining test) and after (posttraining test) training.

Method

Subjects. Subjects were 22 tammar wallabies (18 females and 4 males). They were randomly selected from large breeding groups in the Macquarie University Fauna Park and transferred to individual test yards for the duration of the experiments. Levels of exploration and arousal decreased within a few days of transfer and indicated that each individual settled rapidly into its new environment. While tammars tend to aggregate at feeding patches, they display no social grouping patterns other than a close association between mothers and young at foot (Smith & Hinds, 1995), which is probably why social isolation in captivity does not seem to cause any distress.

Apparatus. During the experiments, each wallaby was held in a small (length 12 m, width 4 m) individual enclosure (Figure 1). The walls of the enclosure were fully screened by black plastic except for three openings. One 1 x 0.4 m opening was located in one of the short sides of the enclosure and allowed the observer to watch and videorecord the animal from a hide abutting the fence; two additional 1.5 x 1 m openings were located in the middle of each of the long sides of the enclosure and behind these were *stages* upon which visual stimuli were presented. A 1 x 0.7 m 'door' in the short side of the enclosure opposite to the hide was used to move stimuli into, and out of, the yard during some training techniques. 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, which was operated by the experimenter from the hide.

Procedure. Each wallaby first received a pretraining test in which I quantified its initial response to the model fox. I then conducted four or eight training trials in which a model fox was paired with an aversive event (see below). After training, the animals underwent a posttraining test in which I again measured their response to the fox. All data were collected within three hours of dawn and three hours of dusk. These are ideal times to conduct trials because tammars forage in the early morning and late afternoon (Blumstein et al., 1999).

The model fox was presented for 60 s on the stage during each pre- and posttraining test. The predator was only presented if the subject was foraging or engaged in another relaxed behavior such as grooming or sitting in a location which afforded it an unobstructed view of the visual stimulus. This procedure controlled both for baseline behavior and the position of the animals when they first saw the model predator. Pre-and posttraining trials were conducted randomly in the morning or in the afternoon.

Each wallaby was randomly assigned to a training treatment. I tested five different training techniques (Table 1). In all methods, the CS was a taxidermically prepared fox. I used a realistic model because this stimulus contained all the morphological features of a predator with which reintroduced wallabies are faced, while enabling me to remove the effect of behavior, which is difficult to control experimentally. Throughout training, an experimenter, referred to in this role as the *keeper*, entered the enclosure once a day to feed the wallaby.

In methods A to D, the subjects underwent training trials in which the fox appeared 3-5 s before a human carrying a net entered the yard and began a simulated capture procedure (Table 1). The appearance of the fox thus reliably predicted the onset of the capture event. Animals were run 4 times back and forth in the enclosure along the fence while the net was held just above the ground, but were never caught. The human then exited the yard and the fox was withdrawn from the animal's sight approximately 2 s later. The whole procedure lasted approximately 60 s.

Table 1
Description of Five Different Training Techniques.

Training technique	CS Location	US Nature	US Location	Keeper Location	Number of trials	Number of subjects
A	Stage	Simulated capture	Hide	Hide	4	4
B	Door	Simulated capture	Door	Door	8	5
C	Door	Simulated capture	Door	Hide	8	4
D	Stage	Simulated capture	Hide	Hide	8	4
E	Door	Alarm thumps	-----	Hide	8	5

Note. See text and Figure 1 for details.

In training technique A (Table 1), the fox appeared on one of the stages and the human entered and exited the yard through the hide window (Figure 1). In methods B and C, I investigated whether increasing the spatial proximity of the CS and the US enhanced learning. In both methods, the fox and the aversive human emerged through the door. Each training trial required approximately 4 minutes of preparation during which the experimenter mounted the fox on the cart and aligned it with the door. These sounds produced a second CS that signaled the imminent capture attempt to the wallaby. I tested whether reducing the predictive value of this cue enhanced learning about the model predator. While in method C, the keeper entered the yard through the hide window, in method B, she entered through the door. In method B, there was thus no predictive relationship between preparation sounds behind the door and the onset of the capture. The appearance of the model fox was hence the only reliable predictor of the simulated capture in this method. In method D, the wallabies underwent the same training technique as in A, but received 8 training trials instead of 4. This enabled me to determine whether increasing the number of training trials enhanced learning.

In method E, the wallabies received training trials in which the model fox was presented in conjunction with a playback of macropod alarm thumps. The model fox was pushed through the door into the yard 3-5 s after the onset of the alarm thump playback. This order of presentation (US-CS) is equivalent to backward conditioning, which is known to produce only low levels of CS-learning (Pavlov 1927). However, I considered that it best emulated a natural situation in which a wallaby hears a conspecific alarm thumping and then searches for, and identifies, the source of alarm. The model remained immobile in front of the door until the end of the alarm thump chorus and was then withdrawn from the yard by pulling it back through the door.

To create the alarm thump playback sequences, I made several recordings of alarm thump choruses in the Fauna Park and digitized them (Digidesign Audiomedia II A/D board, Pro Tools software, sample rate 44.1 kHz, 16 bit amplitude encoding). I then edited the recordings to make four distinct US alarm thump choruses, each of which mimicked the sound of several wallabies moving and alarm thumping. Each chorus lasted 60 seconds. To reduce habituation to the US, each animal heard each chorus only twice, in a random sequence during the course of the 8 training trials. The choruses were played using a PowerBook 570c computer through two Sony SRS-77G powered speakers. The speakers were placed on each side of the enclosure so that the stereo playback simulated wallabies running from one side of the enclosure to the other.

I conducted two training trials per day, one in the morning and one in the evening (methods B-E), but for method A, training trials were conducted in the evening only.

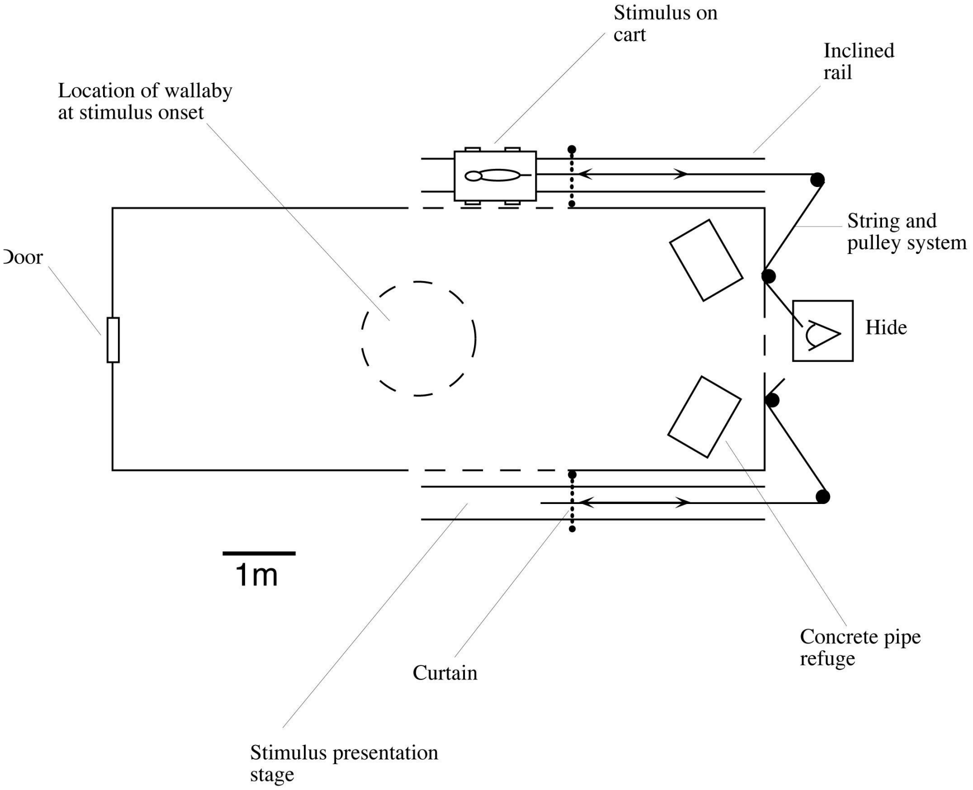

Figure 1. Plan view of an individual test yard. Visual stimuli were presented only if the subject was foraging or engaged in other relaxed behavior in the center of the pen (copyright Griffin et al., 2001).

Data Analysis Procedures. All trials were videorecorded, but only pretraining and posttraining tests were scored and analyzed. I 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.

Behaviors were scored from videotape as vigilance (bipedal stand), relaxed (forage, sit with tail between legs, groom) or locomotion (hop, pentapedal walk). When afraid, wallabies typically suppress relaxed behavior and switch to alternating bouts of vigilance and locomotion. Relaxed behavior is hence an aggregate measure, which is particularly sensitive for quantifying overall antipredator response. Hopping (bipedal locomotion), which is characteristic of a high level alarm response, was also scored separately. Here, I only report results for vigilance, relaxed behavior and hopping, because these were the behaviors most affected by training.

To quantify overall antipredator response to the model fox, I measured changes in behavior from pre-stimulus baseline. The percentage of time spent in relaxed behavior and vigilance was determined for the 60-s baseline and for 24 successive 15-s intervals from stimulus onset to 5 min after stimulus presentation. I then calculated the difference between the percentage of time allocated to relaxed behavior and vigilance during each 15-s time interval and the percentage of time allocated to these behaviors during the 60-s pre-stimulus baseline.

To isolate the effects of training on the animals' responses to the fox, I calculated the mean change in the percentage of time spent in vigilance and relaxed behavior between pre- and posttraining tests (pre/post-response difference) for each 15-s time interval and each training technique. I assessed whether there was significant variation in the effects of all five training techniques using a two way repeated-measures analysis of variance (ANOVA) with factors for training technique (methods A to E) and time (successive 15-s intervals).

In my experimental setting, bouts of hopping only lasted a few seconds at a time because an alarmed state was characterized by rapidly alternating bouts of vigilance and hopping along the fence. This stereotypical response, which typically only occurred immediately after the appearance of the fox, presumably reflected motivation to escape. To obtain sufficient temporal resolution, I analyzed changes in hopping in 5-s time bins. The percentage of time spent hopping was determined for the 60-s pre-stimulus baseline and 6 successive 5-s time intervals starting at fox onset to 30 s afterwards. I then calculated the change in the percentage of time spent hopping between each 5-s interval and baseline. Finally, I calculated the mean pre/post-response difference for each 5-s time interval and for each training technique. I compared the effects of the five training techniques on the animals' behavior by using a two-way repeated-measures ANOVA with factors for training technique (methods A to E) and time (successive 5-s intervals).

All analyses were carried out on non-transformed data using Statview 5.1 (SAS Institute, 1998) and Superanova 1.1 (Abacus Concepts, 1991). I used an alpha level of 0.05 throughout.

Results and Discussion

Formal analyses revealed no differential effect of training technique on any behavior after training (Figures 2 and 3). There were also no significant training technique x time interactions and no main effects of time. However, a visual inspection of Figure 2 suggested that, after training, group A (fox on stage and human through hide) tended to suppress relaxed behavior and increase vigilance more in response to the fox than animals trained with other techniques. Similarly, Figure 3 suggested that group B (fox and human through door) increased hopping at fox onset more markedly than other training groups. It also appeared that the differential effects of method A lasted for about 120 s after stimulus onset, while those of method B waned after only 20 s. High speed locomotion, such as hopping, is characteristic of a higher level alarm response than reduced relaxed behavior and heightened vigilance. Thus, method B caused a change in alarm behavior of a higher intensity, but of shorter duration, than technique A. Failure to detect significant differences between training methods probably reflected my small sample size (4-5 animals per treatment) which provided only limited statistical power. For ethical reasons, I deliberately used a minimal number of animals. I thus selected method A as an optimal training technique because it produced the most sustained increase in the wallabies' antipredator responses.

Interestingly, doubling the number of training episodes (method D) abolished the effects of training technique A on the animals' posttraining responses to the fox (Figure 2), suggesting that wallabies habituated to the simulated capture procedure. This idea is consistent with the observation that subjects resumed relaxed behavior progressively more quickly after each successive training episode. It is possible that the effects of the simulated capture would have been maintained if this event had been intermittently reinforced with a real capture. This finding also raises the possibility that methods B, C, and E might have been more effective if I had only conducted four training episodes with each technique, although it was impractical to conduct an empirical test to determine whether this was so. The fact that increasing the number of training trials seemed to make training less effective reveals that the outcome of training can be counterintuitive. Similarly, the fact that the wallabies might have learnt that they were never caught during the simulated capture shows how readily animals learn about events other than the association between predator and fear. As a consequence, the effect sought by the experimenter is abolished. In sum, the results obtained with method D strongly suggest that it is crucial to investigate systematically the effects of training.

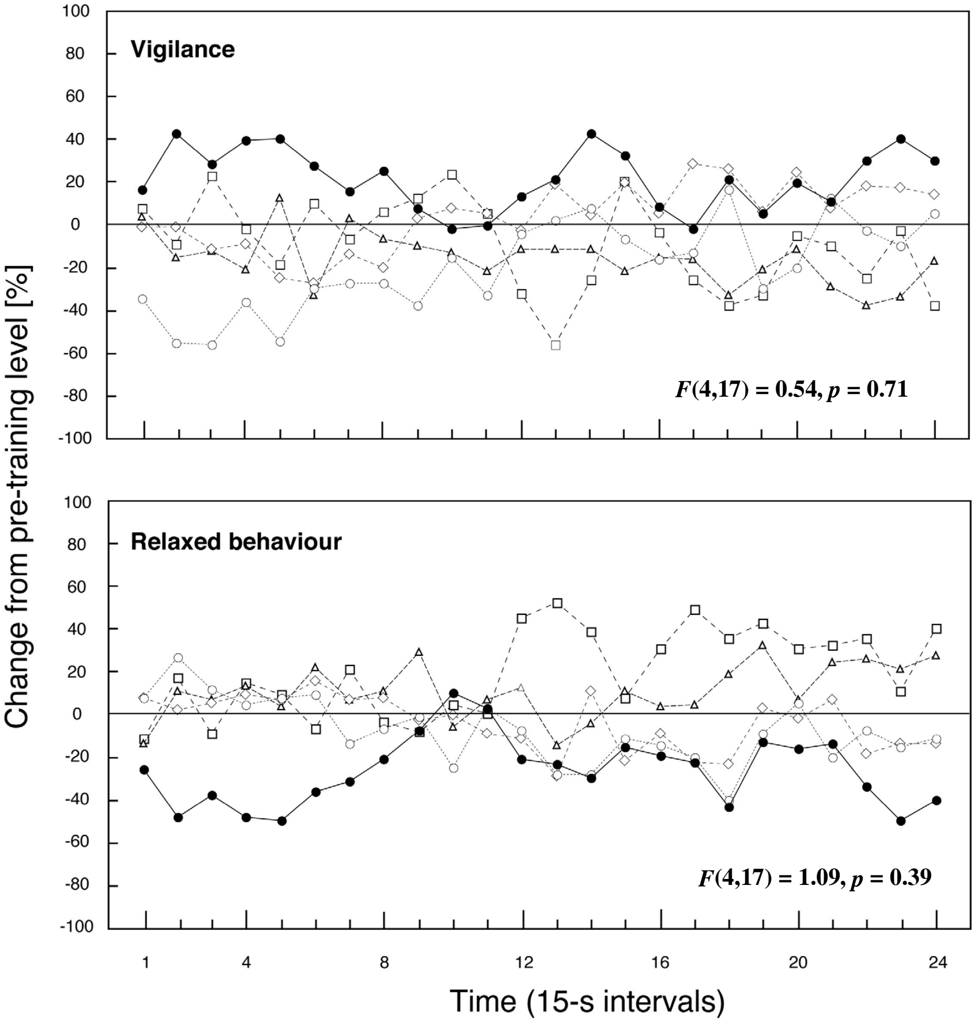

Figure 2. Changes in the responses to a model fox after training. Each group of wallabies was trained with a different technique: A ---●---, B ---○---, C --◊--, D ---□---, E ---Δ--- (see Table 1). The mean difference between the pre-test and the post-test response is shown for 24 successive 15-s time intervals from fox onset, 1 min during fox presentation and 5 min after the predator had disappeared from the stage. The effects of the five different training techniques were compared using a two way repeated-measures ANOVA with factors for training technique (methods A-E) and time (15-s intervals). The *p*-values indicate the significance level for the main effect of training technique.

In training technique B, both the keeper and the aversive human entered the test yard through the door (Figure 1), so preparation sounds behind this opening signaled either the daily ration of food or the simulated capture. The appearance of the fox was hence the only reliable predictor of the aversive US. In contrast, in training technique C, only the aversive human entered the test yard through the door, so sounds behind this opening were a reliable predictor of the simulated capture together with the appearance of the fox. Posttraining responses suggested that technique B inculcated a heightened fear response to the predator while technique C did not (Figure 3). This difference is not attributable to the number of training episodes because both techniques involved eight sessions. It suggests that the availability of a second CS in technique C interfered with learning about the predator. It is possible that the wallabies learnt that the sounds of a human around the enclosure signaled the onset of a capture, rather than the appearance of the fox. I did not formally test whether the subjects acquired a fear response to the sounds of the human, but there is good evidence that such overshadowing can occur in fear conditioning (Kamin, 1969; Mackintosh, 1971). More generally, this result suggests that conditioning to other CSs present in the experimental context may interfere with learning about the target predator. Conditioned stimuli associated with the training procedures per se, such as the experimental environment, will not be predictors of predators in the wild and I recommend that wildlife managers take care to avoid detrimental conditioning to these cues.

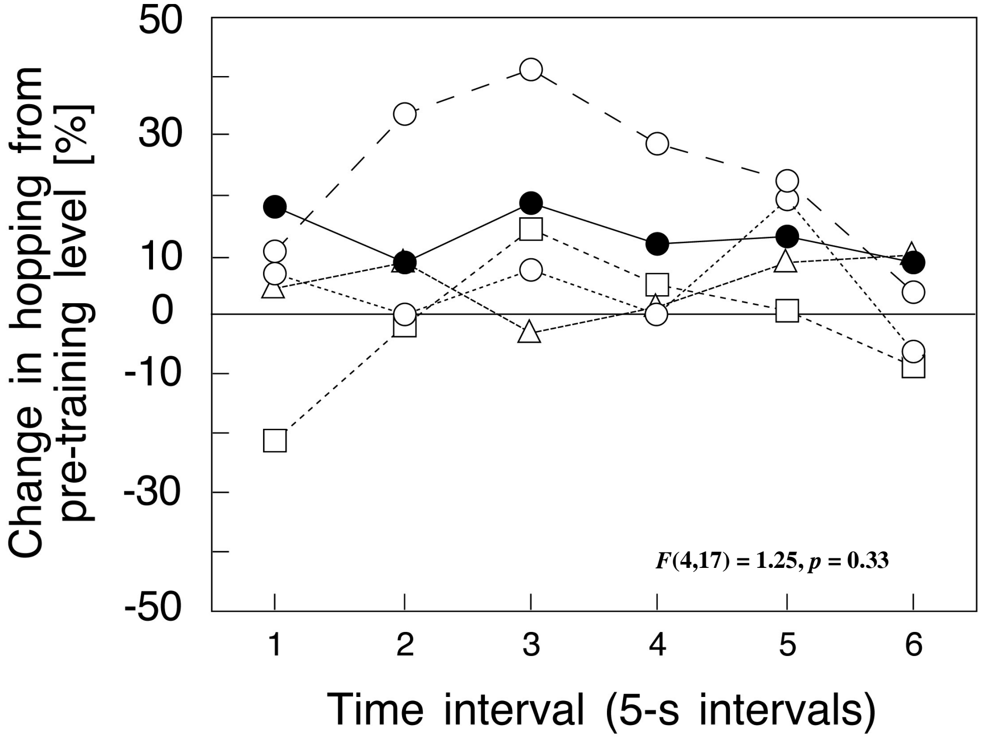

Figure 3. Changes in hopping in response to a model fox after training. Each group of wallabies was trained with a different technique: A ---●---, B ---○---, C --◊--, D ---□---, E ---Δ--- (see Table 1). The difference between the pre-test and the post-test level of hopping is plotted for 6 successive 5-s time intervals from the appearance of the fox model to 30 s afterwards. The effects of the five different training techniques were compared in the same way as for Figure 2. The *p*-value indicates the significance level for the main effect of training technique.

Wallabies that experienced paired presentations of the model fox and a playback of macropod alarm thumps tended to show lower responses to the fox following training than before (Figure 2). Learning about a CS may fail if the aversive US is not effective. The sound of macropod alarm thumps is known to elicit heightened vigilance and to suppress foraging in tammar wallabies (Blumstein et al., 2000), demonstrating that this alarm signal is inherently salient. Consequently, it is unlikely that associating the model fox with the sound of alarm thumps failed to enhance the animals' responses because the US was not salient, but rather because the wallabies habituated to it. Given the inherent salience of this social signal, I suggest that alarm thump playbacks have the potential to be an effective aversive US providing they are used in conjunction with more aversive USs and the number of training episodes is low.

In conclusion, the present experiment strongly suggested that the degree to which animals acquire fear of a predator is dependent upon subtle variations of training method. Testing the effects of several different training techniques allowed me to select the method that produced the largest increase in the responses of tammar wallabies to a model fox. This technique consisted of four presentations of the predator on the stage, paired with a human who emerged through the hide window and began a simulated capture procedure. This technique was used in subsequent experiments.

Experiment 2: Specificity of Learning

In Experiment 1, the effect of training was isolated by measuring the change between the animals' pretraining and posttraining responses to the fox, an experimental design widely used in the predator avoidance training literature (e.g., McLean et al., 2000). While an increase in response indicates an effect of intervening experience, it does not in itself demonstrate that the wallabies learnt the association between the predator and the simulated capture, or that acquired responses were specific to the fox. Such changes in behavior can be mediated by a general increase in arousal and/or repeated exposure to aversive USs, neither of which involve learning about the predator. While most antipredator training studies have found evidence for changes in behavior after training (e.g., McLean et al., 1996; Miller et al., 1990), to my knowledge none was designed to describe fully what the animals had learnt.

I review here an experiment that was designed to explore the nature of the behavioral changes observed after training in Experiment 1. The antipredator responses of tammar wallabies were enhanced by conducting four paired presentations of the predator and a simulated capture, the training technique developed in Experiment 1. To determine whether the tammars' acquired responses were specific to the fox, I quantified responses to an array of visual models, both before and after training. The design also incorporated an unpaired control group, in which animals had identical total exposure to the fox and human, but with no predictive relationship between these two stimuli. Comparisons between the responses of the paired and unpaired groups were conducted to isolate changes attributable specifically to learning 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 simulated capture (Shettleworth, 1998). This design also enabled me to ensure that learning was a consequence of the contingency between the predator and the simulated capture, rather than a consequence of temporal contiguity only (see Shettleworth, 1998).

Method

Subjects were 16 tammar wallabies (eight males and eight females). For training, they were randomly assigned to the paired (experimental) or explicitly unpaired (control) group. The paired group underwent training trials in which the fox appeared on the stage 3-5 s before a human carrying a net emerged through the hide and began a simulated capture procedure. In this group, the appearance of the fox thus reliably predicted the onset of the capture event. The unpaired control group also underwent four simulated capture procedures and was presented with the fox four times, 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 the trials, the animals saw the fox first and in the other half they experienced the simulated capture first. For this group, there was thus no predictive relationship between fox and an aversive event.

During pre- and posttraining tests, I measured each animal's response to an array of stimuli. Four taxidermic mounts were selected to tease apart the effects of training, familiarity, and predatory threat on acquired responses. A model fox was an unfamiliar predator and also the predator with which the animals were trained. To determine whether the effects of fox training generalized to another morphologically similar predator, the subjects were presented with a model cat. A model juvenile goat (*Capra hircus*) made it possible to compare acquired responses to a predator with those to a non-predator without the confound of novelty because both stimuli were novel to the wallabies. Finally, a conspecific wallaby was used to measure responses to a stimulus that was neither a predator, nor unfamiliar. Responses to the mounts were compared with those evoked during blank control trials, in which no stimulus was presented. These trials quantified general changes in behavior associated with training. The cart was also presented alone to measure the proportion of response attributable to the presentation device and its associated movement.

Data were collected and analyzed in the same way as in the previous experiment. As before, responses to each stimulus were quantified by measuring changes in behavior from pre-stimulus baseline in 15-s time intervals. The effect of training was isolated by calculating the mean pre/post-response difference for each group, stimulus and time interval. The mean pre/post-response difference of the paired-experimental group was compared to that of the unpaired control group using a two way repeated-measures ANOVA with factors for group (experimental and control) and time (15-s intervals). These analyses were conducted separately for each of the six pre-/post-testing stimuli. For the purpose of this review, I only report changes in relaxed behavior which is an aggregate measure that quantifies overall antipredator response. A more detailed description of the results can be found elsewhere (Griffin et al., 2001).

Results and Discussion

After training, the wallabies for which the fox had predicted the onset of the simulated capture suppressed relaxed behavior in response to the model fox significantly more than those in the unpaired group (Figure 4). The paired group showed a very similar fear response to the model cat even though this predator had never been paired with the aversive event. In contrast they did not change their behavior in the presence of the goat. There were also no differences between the two groups in response to the cart or during the blank control, demonstrating that the presentation device, to which the fox was attached, was not sufficient to evoke the acquired response and that training did not cause a general increase in arousal.

This pattern of results demonstrated that changes in behavior after training were a consequence of associative learning; wallabies became more fearful of the fox because they learnt that its appearance signaled the onset of the capture. These results also demonstrated that acquired responses were specifically evoked by the predator with which they were trained and by another morphologically similar predator. Results are encouraging for those engaged in the design of prerelease preparation programs for endangered species. Previous attempts to inculcate a fear response using a human as an aversive US have been unsuccessful (McLean et al., 2000). Comparisons with this study suggest that the human is likely to have overshadowed the target predator because these two events were presented simultaneously. This finding is consistent with results from Experiment 1, which suggested that the probability of learning is sensitive to fine details of the training protocol adopted.

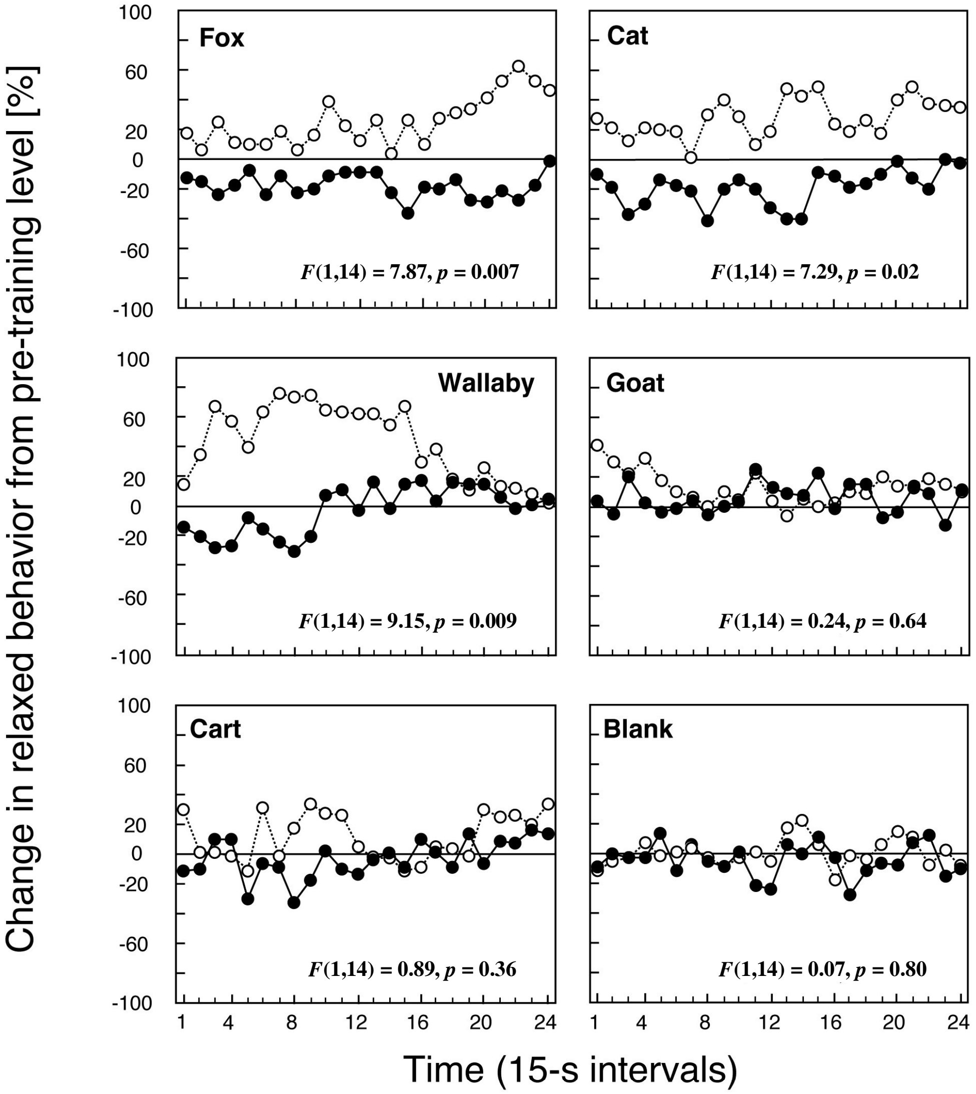

Figure 4. Changes in relaxed behavior after training for the paired-experimental (---●---, $N = 8$) and unpaired-control (---○---, $N = 8$) groups. Mean differences are calculated in the same way as for Figure 2. For each stimulus, mean responses of the paired and unpaired wallabies were compared using a two way repeated-measures ANOVA with factors for group (paired vs. unpaired) and time (15 s time intervals). The p-values indicate the significance level for the main effect of group (copyright Griffin et al., 2001).

Surprisingly, there was also a significant difference between the paired and the unpaired group in response to the conspecific wallaby after training (Figure 4). A significant Group x Time interaction ($F_{(23,322)} = 3.458$, $p < 0.001$), which was present for this stimulus only, indicated, however, that the change in behavior was quite brief, and contrasted with the sustained response to the two predators. It is conceivable that the behavior of social companions provides contextual cues about the likelihood of predation, which may explain why the experimental group attended more to the conspecific model after training. Although consistent with earlier findings on the social behavior of tammars in the predatory context (Blumstein et al., 1999, 2000; Griffin & Evans, in press), this idea remains to be tested. In the meanwhile, acquired responses to stimuli other than the target predator are likely to decrease the effectiveness of predator avoidance training (Griffin et al., 2001). For this reason, I examined in the next experiment whether discrimination training could be used to eliminate this transient response.

Experiment 3: The Role of Discrimination Training

Discrimination training in which some stimuli are reinforced, and others are not, is a widespread technique in classic studies of learning. It is used traditionally to enhance responses to one stimulus and decrease those to another. Experiment 2 demonstrated that wallabies became more fearful of the model fox after training. However, the animals also showed a transient increase in response to a conspecific wallaby. Here, I review briefly an experiment that was designed to test whether differential reinforcement of the fox and the wallaby enhanced the specificity of the acquired antipredator response. It also examined whether generalization from fox to cat was sufficiently robust to resist the effect of habituation.

Method

Subjects were 16 tammar wallabies (eight males and eight females). For training, each individual was randomly assigned to the paired (experimental) or explicitly unpaired (control) group. In addition to paired (experimental group) or unpaired (control group) presentations of the fox and simulated capture, each group received four presentations of the model cat alone and four presentations of the conspecific model alone. During pre- and posttraining tests, I measured each animal's response to the model fox, cat, conspecific wallaby and during a blank control. Data were collected and analyzed in the same way as in the previous experiment. For the purpose of this review, I only present changes in relaxed behavior.

Results

Wallabies for which the fox had predicted the onset of the capture suppressed relaxed behavior significantly more in response to the fox than the control group (Figure 5). Furthermore, they showed the same acquired fear response to the cat, despite repeated, nonreinforced presentations of this model during training. In contrast, there were no differences between the two groups in response to the wallaby, despite repeated presentations that were identical to those conducted with the cat. There were also no differences between paired and unpaired groups during the blank control, demonstrating that training did not produce a general increase in arousal.

After training with the fox only (see previous experiment), subjects showed a brief increase in response to a conspecific wallaby, which was reflected by a significant group x time interaction for this stimulus. There was no such interaction for the conspecific model, or for any other stimulus, after discrimination training. Differential reinforcement of the fox and the wallaby hence subtly enhanced the specificity of the acquired response. There have been no previous attempts to use differential reinforcement of predatory and nonpredatory stimuli in antipredator training. The present findings suggest that this technique could be used to enhance the specificity of learning in cases where it is low. Results also revealed that repeated non-reinforced presentations of the cat did not counteract the effect of response generalization from the fox, demonstrating that this effect is robust. Such generalization could make predator avoidance training more time effective because animals may not require coaching for every predatory species they will subsequently encounter.

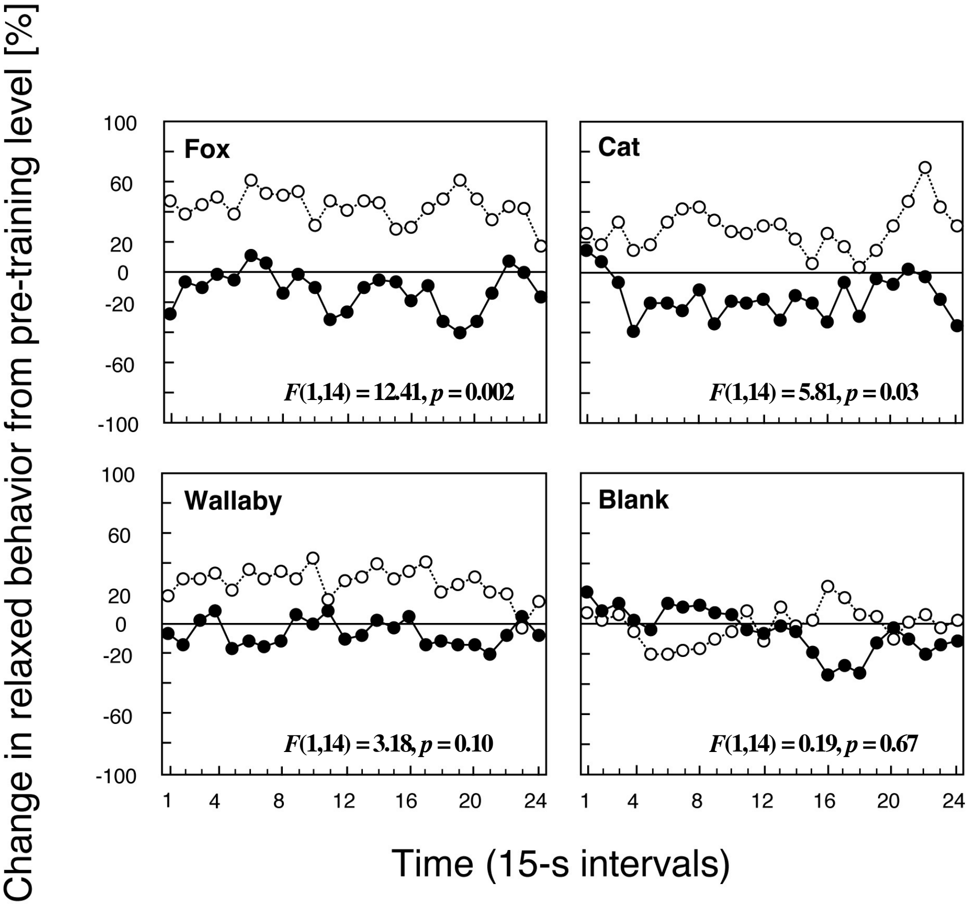

Figure 5. Changes in relaxed behavior after discrimination training for the paired-experimental (---●---, $N = 8$) and unpaired-control (---○---, $N = 8$). Mean responses of the paired and unpaired wallabies were compared in the same way as for Figure 4. P-values indicate the significance level for the main effect of group (copyright Griffin & Evans, 2003).

Discussion

In this series of experiments, I drew upon the principles established by over a century of empirical work on animal learning to design a training technique that enhanced the responses of tammar wallabies to a target predator. I then used controlled experimental protocols to describe the content of learning and to test the effect of discrimination training. I found that training can inculcate a fear response that is specific to predators, but the likelihood of learning is dependent upon details of the protocol adopted. I also found that differential reinforcement of predatory and non-predatory stimuli has the potential to enhance the specificity of learning, if required. Together these findings suggest that these wallabies have a sophisticated antipredator behavioral system in which genetic predispositions and experience interact to allow them to cope with predators, as well as adjust to novel ones. These properties make antipredator training more likely to succeed (Griffin et al., 2000).

Future experimental reintroductions in which the survival rate of trained tammars is compared with that of individuals that have received no training will establish whether fox-fear acquired in captivity enables wallabies to avoid this predator after release.

The resources allocated to conservation programs for endangered species are often insufficient to conduct extensive research. Nevertheless, I encourage wildlife managers to identify the content of learning, by incorporating adequate control groups and control stimuli into experimental protocols, whenever possible. I tested the effects of five different training techniques which differed only slightly from each other; yet only one seemed to inculcate a sustained fear response to the target predator. While this conclusion must remain tentative because formal analyses did not reveal any significant difference between this technique and the others, it nevertheless suggests that failure to produce learning might be a common outcome of training. Many species, from insects to primates, are able to acquire information about predictors of biologically important events, but these stimuli are not always those controlled by the experimenter (Breland & Breland, 1961). This is an important consideration for those engaged in predator avoidance training. If postrelease survival tests are conducted without identifying the content of learning, they may lead to the, perhaps erroneous, conclusion that training does not improve survival. The problem may instead be that the animals learnt nothing during training.

I suggest that evaluating the content of learning will also be the most fruitful approach to the study of antipredator training in the long term. It is possible to investigate the effects of predator avoidance training by focusing on postrelease survival, and tests may reveal that one technique has a beneficial effect, while another has none (van Heezik et al., 1999). However, the question of why one training protocol works, while the other does not, remains unanswered. In contrast, if it is known that the successful technique inculcated a fear response that is specific to predators, while the second produced only a general increase in arousal, postrelease survival tests will establish that animals have to learn about the predator to cope with it after release. We can then set out to design techniques that maximize learning about the predator. Alternatively, if tests reveal that a general increase in wariness improves survival, perhaps by enabling animals to avoid predation in the critical phase immediately after release, we should aim to develop more simple techniques that do not involve presenting predator stimuli.

The benefits of a controlled experimental approach to the study of predator avoidance training are particularly well illustrated in fish. Large numbers of hatchery-reared juveniles are released each year to supplement natural populations available to the fishing industry (Brown & Laland, 2001). Mortality rates of hatchery-reared young are considerably higher than those of wild-reared individuals (Maynard et al., 1995) and predation is the principal cause of death (Howell, 1994). Antipredator training has the potential to make these individuals more predator-aware and to improve their survival. The design of antipredator training techniques has benefited hugely from the procedures and findings from basic work on predator recognition learning (Brown & Laland, 2001). In particular, the findings that (1) socially acquired predator avoidance is a widespread phenomenon (Magurran, 1989; Suboski et al., 1990), (2) social training inculcates recognition of the target predator (Chivers & Smith, 1994; Chivers et al., 1995), (3) acquired predatorawareness can propagate through a population (Chivers & Smith, 1995), and (4) learning enhances the likelihood of survival (Mirza & Chivers, 2000) has encouraged the development of antipredator training programs. There is an urgent need to study predator avoidance learning in birds and mammals with the same careful experimental approach.

For obvious reasons, studies of the kind presented here are often difficult to undertake with endangered species, if only because subject numbers are limited. One possible approach is to develop training techniques using phylogenetically related species that are not endangered (Miller et al., 1990). For example, the tammar wallaby is likely to be a useful model species for other macropods, such as the black-striped wallaby (*Macropus dorsalis*), which shares a similar ecology and life style with the tammar (Kirkpatrick, 1995) and is phylogenetically closely related (Taylor et al., 1999).

I also encourage experimental psychologists to undertake studies of learning using biologically meaningful stimuli, such as predators. The acquisition of predator avoidance behavior, in particular, constitutes an exciting area of research because it puts the study of learning into an explicitly evolutionary and functional framework. There is still a wealth of questions to be addressed, most of which can be studied in controlled experimental environments. For example, we need to test the effects of different aversive USs and make sure that acquired fear responses are expressed in other environments than the training context. Social transmission of acquired responses is another important aspect of antipredator training that requires attention because it will increase substantially the effectiveness of training in species in which it occurs. The results from very recent experiments suggest that trained tammar wallaby demonstrators can socially transmit their acquired fear response to predator naïve observers (Griffin & Evans, in press). Such findings will be of interest to both the study of animal cognition and conservation programs for endangered species.

In conclusion, the work of both experimental psychologists and conservation biologists has the potential to improve our understanding of how birds and mammals learn about predators. Combined efforts should soon establish whether predator avoidance training is a useful wildlife management tool.

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