



Social learning of antipredator behaviour in a marsupial

ANDREA S. GRIFFIN*† & CHRISTOPHER S. EVANS*

*Animal Behaviour Laboratory, Department of Psychology, Macquarie University

†Cooperative Research Centre for the Conservation and Management of Marsupials, Sydney, Australia

(Received 19 June 2002; initial acceptance 25 July 2002;
final acceptance 26 November 2002; MS. number: 7378R)

Socially acquired predator recognition has been demonstrated in a range of taxa, but there is no experimental evidence for this phenomenon in marsupials. We have previously shown that tammars wallabies, *Macropus eugenii*, can be individually trained to avoid a model fox, *Vulpes vulpes*. Here, we examined whether such acquired responses can be socially transmitted to predator-naïve companions. Tammars were given training trials in which they observed the response of a demonstrator wallaby that was either fearful of the fox (experimental group), or indifferent to it (control group). Tammars in the experimental group subsequently responded to the fox model with significantly higher vigilance levels than controls. To examine the specificity of this acquired antipredator behaviour, we measured responses to an array of other visual stimuli after training and compared these with the results of identical pretraining tests. There was a small difference between the two groups in responses to a model cat, *Felis catus*, but not to a model nonpredator (goat, *Capra hircus*). There were also no differences between experimental and control groups during blank trials, in which no stimulus was presented, showing that the elevated vigilance response to the fox did not simply reflect a general increase in arousal. The effect of training was hence to inculcate a relatively specific response to the fox, with only limited generalization to another predator stimulus. These findings provide the first evidence for social learning in a marsupial and suggest that this group has cognitive characteristics convergent with those of eutherian mammals.

© 2003 Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour.

Perhaps surprisingly, predator recognition in many animals depends upon experience (reviewed by Griffin et al. 2000). Observational conditioning plays a primary role in this process (Cook et al. 1985; Suboski 1990). In this form of learning, individuals associate a previously neutral event with the affective state evoked by a social cue (e.g. alarm responses of a companion). For example, Mineka & Cook (1988) found that juvenile rhesus monkeys, *Macaca mulatta*, acquired a fear response to snakes after watching other adults respond fearfully to them. Similarly, fish respond with antipredator behaviour to chemical substances released from the damaged skin of conspecifics and this experience facilitates learning (Magurran 1989; Chivers et al. 1995).

There is increasing interest in exploiting the potential for animals to learn about predators to address practical problems, particularly in conservation programmes and the fishing industry. In both contexts, captive-bred predator-naïve individuals are released into the wild, but

survival rates are currently low. Predation has been implicated as a significant cause (e.g. Short et al. 1992; Brown & Laland 2001). Although training regimes that take advantage of social learning are widely used with fish, other animals are typically trained individually by presenting a target predator in conjunction with an aversive experience (e.g. McLean et al. 1999, 2000). In species where predator avoidance is normally acquired socially by observing the behaviour of companions, social training regimes may be more effective because they emulate natural processes. In addition, social transmission of individually acquired predator avoidance has the potential to amplify the effects of an initial training intervention (Curio 1988; Suboski 1990) by causing adaptive responses to spread through a population.

Socially acquired predator avoidance has been described in birds, fish and primates, but there have been no tests for this phenomenon in marsupials. This group diverged from placental mammals 98 million years ago (Springer et al. 1994) and many species are ecologically convergent with their eutherian counterparts. Although sociality is often thought to be the principal life history variable favouring the evolution of social learning, several theoretical and empirical studies suggest that

Correspondence and present address: A. Griffin, Department of Biology, McGill University, 1205 avenue Docteur Penfield, Montreal, Quebec H3A 1B1, Canada (email: andrea@galliform.psy.mq.edu.au). C. S. Evans is at the Department of Psychology, Macquarie University, Sydney, NSW 2109, Australia.

other ecological factors, such as the predominance of scramble competition, may play a determining role (Klopfer 1961; Boyd & Richerson 1988; Lefebvre & Palameta 1988; Lefebvre et al. 1996). Comparative studies of distantly related, yet ecologically convergent, species have the potential to provide insights into the relation between life history and environmental variables and the evolution of social learning.

An improved understanding of predator recognition mechanisms is also important for conservation. On mainland Australia, where marsupials represent the predominant fauna, introduced foxes, *Vulpes vulpes*, and feral cats, *Felis catus*, pose a major threat; about 20% of species and subspecies in the small and medium-sized range are either extinct or severely threatened (Maxwell et al. 1996). Reintroductions and translocations are common conservation management procedures (Maxwell et al. 1996) and there is an urgent need to develop preparation procedures that will maximize postrelease survival.

Tammar wallabies, *Macropus eugenii*, are a medium-sized (4.5–7.0 kg), moderately social species of Australian macropod. Tammars aggregate at feeding grounds (Croft 1989), which provides opportunities for social learning. Alarmed individuals have characteristic antipredator responses, including fleeing, alarm foot thumping, alert body posture and fixation of the threatening stimulus (Blumstein et al. 2000; Griffin et al. 2001). Such social cues have the potential to trigger learning in naïve individuals.

In an earlier study (Griffin et al. 2001), we successfully enhanced the antipredator responses of tammar wallabies to a model fox by presenting it in conjunction with a human who simulated a capture attempt. A control group of wallabies became less fearful of the fox after they had had identical total exposure to model and human, but with no predictive relationship between those two stimuli.

In the present study, we tested whether such acquired responses could be socially transmitted from a previously trained tammar to a predator-naïve observer wallaby. During training, observer wallabies from an experimental group watched a fox-fearful demonstrator wallaby respond to the fox with fleeing and obvious antipredator behaviour. Animals in a control group watched a fox-habituated wallaby, which was indifferent to the predator model. To quantify the effects of training and to determine whether changes in the behaviour of observer wallabies were specific to the fox, we measured the responses of each observer wallaby to the target predator and to an array of other visual models, both before and after training.

METHODS

Subjects and Husbandry

We used only females, to reduce the likelihood of aggressive interactions between unfamiliar wallabies. Animals were removed temporarily from large breeding colonies in the Macquarie University Fauna Park and returned at the end of testing. While in social groups, the

wallabies were held in enclosures (30 × 30 m), which contained one male and about 15 females. The wallabies had access to food (kangaroo pellets) and water ad libitum. Group housing pens had natural vegetation and were provided with concrete pipes for additional shelter.

Observer wallabies

We selected 16 unrelated adult female tammar wallabies as observers. Five females had been caught on Kangaroo Island off the southern coast of mainland Australia, which is a fox-free environment, and had been in captivity for at least 2 years before this experiment. The other 11 tammars were captive bred. All wallabies had been caught and handled regularly. We have documented the antipredator behaviour of tammar wallabies in several studies and have found no differences between wild-caught and captive-bred individuals (D. T. Blumstein, unpublished data). To our knowledge, none of the wallabies used as observers had been in contact with foxes, but cats are seen occasionally within the Fauna Park.

Demonstrator wallabies

Eight females had been trained in our earlier study (Griffin et al. 2001), which took place from 4 to 7 months before the present experiment. Of these, we selected seven to serve as demonstrators. The four 'fox-fearful' animals had become wary of a model fox because they had learned that it predicted the appearance of a human with a net. In contrast, the three 'fox-indifferent' wallabies had become less fearful of the fox model because they had habituated to presentations that took place at different times from capture attempts. The eighth female from the previous study was not used because her responses to the fox were unaffected by training. Because only seven demonstrators were available for 16 observers, we used several wallabies repeatedly in this role (range 1–4 times). Statistical analyses were designed to take account of the nonindependent nature of scores from observer wallabies that were assigned the same demonstrator (see Statistical methods).

Animals were housed under a New South Wales National Parks and Wildlife Service Permit. All husbandry and experimental procedures were approved by the Macquarie University Animal Ethics Committee.

Individual test yards

During experiments, each wallaby was held in an individual test yard. These were wire-fenced enclosures (12 × 4 m; Fig. 1) with two large concrete pipes (length 1 m, diameter 0.70 m) for shelter. The fence was screened with a 2-m-high strip of opaque black plastic 'weedmat', so that the animal could not see its surroundings. An opening (1 × 0.4 m) in the plastic on one of the short sides of the enclosure allowed the observer to watch and videorecord the animal from a hide abutting the fence. There were also openings (1.5 × 1 m) in the middle of each of the long sides of the enclosure, and behind these were stages on which visual stimuli were presented (Fig. 1). The fence in front of each stage was painted black to

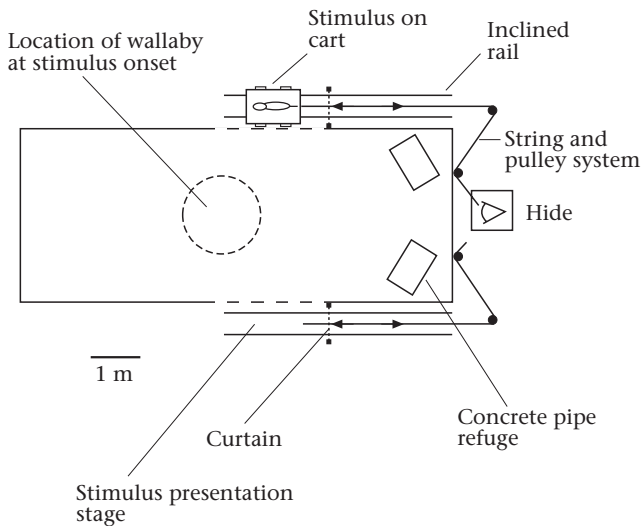


Figure 1. Plan view of an individual test yard. Concrete pipes provided the wallabies with shelter. Visual stimuli were presented only if the subject was foraging or engaged in other relaxed behaviour in the centre of the pen (see text for details). (Reproduced with permission from Griffin et al. 2001.)

reduce light reflection and optimize visibility through the wire. Stimuli were fixed to a cart that ran on inclined rails; the experimenter could pull the cart quietly on to and off the stages by means of a string and pulley system, from the hide (Fig. 1). Curtains hanging perpendicular to the rails on each side screened stimuli from the wallaby before and after presentations.

Stimulus models

We used a range of taxidermically prepared vertebrate models of approximately equivalent size. A fox was selected to represent an unfamiliar predator and was also the model with which the animals were trained. To determine whether the effects of fox training generalized to another species of predator, we used a model cat. A model juvenile goat enabled us to compare responses to a predator and a nonpredator without the confound of novelty, because both the fox and the goat were initially unfamiliar. Tamar wallabies are able to discriminate between these stimuli on the basis of morphological cues alone (Blumstein et al. 2000; Griffin et al. 2001). Responses were compared with those evoked during a blank control trial, in which no stimulus was presented and the presentation device was not activated; this allowed us to quantify general changes in spontaneous behaviour associated with training.

Experimental Protocol

Preparation of demonstrator wallabies

Each demonstrator wallaby underwent two to seven training trials, which were designed to reinforce the effects of earlier training (Griffin et al. 2001) and to verify the expression of either high (fox-fearful) or low (fox-indifferent) levels of antipredator behaviour. In cases where the same demonstrator was used repeatedly in this

role, the wallaby underwent this preparation protocol each time it participated in the experiment. We thus ensured that the quality of the demonstration was consistent, despite repeated use of some individuals. Fox-fearful wallabies were shown the model fox, followed immediately by a simulated capture attempt. Fox-indifferent wallabies saw the same model, but without any aversive experience. Animals in each demonstrator category had to reach a fox-response criterion before being transferred to the yard of an observer wallaby. Fox-fearful wallabies were required to hop away from the model as soon as it appeared and to remain vigilant for at least 3 min after the simulated capture. They reached this criterion within two to three trials (mean 2.9 trials, range 2–4). In contrast, fox-indifferent wallabies were required to remain still when the model appeared and to resume relaxed behaviour such as foraging, grooming or sitting within 45 s. This criterion was reached within four to five trials (mean 4.75 trials, range 2–7).

Acclimatization of observer wallabies

We first habituated each observer 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. Most animals learnt to forage while being observed within 4–5 days (mean 4.8 days, range 3–8). Behavioural testing began once the animal had come to feed on two consecutive occasions.

Behavioural testing

We ran two pre-post-training trials per day, one in the morning and one in the evening. Training trials were conducted once per day, in the evening. Each individually held observer wallaby first received four randomly ordered pretraining trials, during which we quantified its initial response to the stimulus models and during the blank control. We then introduced a demonstrator wallaby into the yard and left both animals undisturbed for 48 h. Four training trials were then conducted in which a model fox was presented on one of the stages. This number of pairings and duration of experience are sufficient to produce learning when animals are individually trained (Griffin et al. 2001). The demonstrator wallaby was removed from the test yard on the same evening, within 2 h of the last training trial. We began post-testing next morning. Each observer wallaby underwent four post-training trials in which it was shown the same set of stimuli as in the pretraining trials, but in a different random order. Throughout the study, the stage on which the stimulus appeared was alternated from trial to trial to reduce the likelihood of habituation.

Test procedure

We collected all data within 4 h of sunrise or sunset to correspond with the peak periods of diurnal foraging activity (Blumstein et al. 2000). In each pre- and post-training trial, a single stimulus was presented on the stage for 60 s. We presented stimuli only if the subject was foraging or engaged in other relaxed behaviour, such as

grooming or sitting. This controlled both baseline behaviour and the location of the animals when they first saw the models. If the wallaby had not come to feed within 2 h, the trial was postponed until the next scheduled test time. However, trials were not postponed for more than 2 days, to control for maximum time interval between successive stimulus presentations.

During training trials, we presented the model fox to each demonstrator–observer pair for 60 s. Although food was deposited at the centre of the yard before each trial, we did not require the animals to be foraging prior to stimulus presentations. During these trials, each observer wallaby had the opportunity to view the predator model in conjunction with the response of a demonstrator wallaby.

It is important to note that the observers in the experimental and the control groups had identical total exposure to the fox. The only difference between these treatments was that the experimental animals saw the predator paired with the response of a fearful demonstrator, whereas the control animals saw it paired with the response of an indifferent one. Planned comparisons between the two groups' post-training responses to the fox, and to other stimuli, thus allowed us to detect changes specifically attributable to the behaviour of the demonstrator wallabies. This design effectively separates socially acquired antipredator behaviour from other effects that might be a consequence of shared experiences, such as confinement in the test yards and repeated exposure to predator models.

Analysis of Behavioural Responses

We videorecorded the wallabies during pre-/post-training trials for 1 min immediately before stimulus presentation (baseline), 1 min during the stimulus presentation, and 5 min after the stimulus had disappeared from the stage. During training trials, we videorecorded the animals for 1 min during stimulus presentation and 4 min after the fox had disappeared. In both kinds of trial, the 3–5-s interval during which the stimulus was moving along the track, but not yet visible to the animals, was excluded from analyses.

We scored test videorecordings using continuous sampling to 0.1-s resolution with The Observer 3.0 (Noldus Information Technologies 1995). For pre- and post-training trials, we quantified changes in time budgets from baseline because animals were consistently foraging before stimulus presentations. Because this was not the case for training, we report absolute time budgets for the period after appearance of the fox model.

Pre- and post-training trials

We concentrated on vigilance (bipedal stand) because an increase in the level of this behaviour would clearly be adaptive in the presence of a predator. The percentage of time allocated to vigilance 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 prestimulus baseline. To quantify

the effects of training, we calculated the change in the percentage of time spent in vigilance between pre- and post-training trials (pre/postresponse difference) for each stimulus, group and 15-s time interval. We compared the experimental observers' mean pre/postresponse difference to that of the control observers, using a two-way repeated measures ANOVA with factors for group (experimental and control observer wallabies) and time (24 successive 15-s time intervals). These analyses were conducted separately for each of the four pre-/post-test stimuli.

Training trials

We analysed training trial videotapes from each demonstrator–observer pair. First, to confirm that the demonstrations experienced by experimental observers differed reliably from those experienced by the control observers, we scored the behaviour of each demonstrator wallaby. For each training trial, we obtained the percentage of time allocated to vigilance, relaxed behaviour (forage, sit with tail between legs, groom) and locomotion (hop, pentapedal walk) from the appearance of the fox model to 5 min afterward. We then compared the mean percentage of time allocated to each behaviour by fox-fearful demonstrators and fox-indifferent demonstrators, using two-way repeated measures ANOVAs with factors for group (demonstrator type) and training trial (four training trials).

To determine whether wallabies in the experimental group were more likely to hear alarm thumps than control animals, we also examined the likelihood of this response in fox-fearful and fox-indifferent demonstrators. Because alarm thumping is relatively rare, we used a nominal score for presence or absence of this behaviour during training tests and then compared the behaviour of fox-fearful and fox-indifferent demonstrators, using a Fisher's exact probability test for a 2×2 contingency table.

Second, we determined whether the behaviour of the observer wallabies reflected that of the demonstrators with which they were housed during training. For each training trial and each observer wallaby, we obtained the percentage of time allocated to vigilance from the appearance of the fox model to 5 min afterward. To determine whether the behaviour of experimental observers differed significantly from that of controls, we compared the mean percentages of time allocated to vigilance by each group, using a two-way repeated measures ANOVA with factors for group (experimental and control observers) and training trial (four training trials).

Finally, we examined whether the behaviour of the observers during training was correlated with that of demonstrators. We calculated the mean time allocated to vigilance across four training trials for each wallaby and then performed a simple regression with values obtained from all demonstrator–observer pairs. To determine whether the strength of this relation changed over the course of training, we also examined the correlation between demonstrator and observer behaviour in the first two training trials and in the last two trials separately.

Statistical methods

Analyses were carried out on untransformed data using Statview 5.1 (SAS Institute 1998), Superanova 1.1 (Abacus Concepts Inc. 1991) and Stata (StataCorp 1999). In each data set, some data points were not fully independent because of reuse of demonstrators. We addressed this problem by using throughout a generalization of Huber and White's estimator of variance (Huber 1967; White 1980, 1982), as implemented by the statistical package Stata (StataCorp 1999). This method (also known as the sandwich, or robust, estimator of variance) adjusts for lack of independence by basing calculations on the clustered rather than on the individual observations. Degrees of freedom in statistical comparisons are hence appropriately reduced, to control Type I error.

Tests for which we had a priori predictions were one tailed. These included (1) between-group comparisons of demonstrator behaviour during training which were conducted to verify that fox-fearful wallabies did indeed engage in higher levels of antipredator behaviour than the fox-indifferent ones; (2) regression analyses of responses during training which were expected to reveal that vigilance levels of individual observers were positively correlated with those of the demonstrator wallabies with which they were housed; (3) comparisons of post-training responses to the fox in the experimental versus the control observer wallabies, in which we predicted higher levels of antipredator behaviour in the experimental group. All other analyses were two tailed. We used an alpha level of 0.05 throughout.

RESULTS

Experimental observers, which watched the model fox in conjunction with the response of a fox-fearful demonstrator wallaby, had an experience that was reliably different from that of control observers, for which the fox was paired with the response of a fox-indifferent wallaby. Fox-fearful demonstrator wallabies allocated significantly more time to vigilance (Fig. 2, Table 1) and locomotion (Table 1) and significantly less time to relaxed behaviour (Table 1) than fox-indifferent ones. They were also significantly more likely to alarm thump (Fisher's exact test: $P < 0.001$). Although there was a decrease in the mean level of locomotion over the course of training (Table 1), demonstrator wallabies maintained their levels of vigilance (Fig. 2) and did not increase their levels of relaxed behaviour (Table 1). The behaviour of the two classes of demonstrators was hence reliably different, and remained relatively constant over the training period, as required by our experimental design.

Comparisons between experimental and control observer wallabies revealed no difference in mean vigilance levels during training (Table 1), but wallabies in the experimental group had a significantly greater post-training response to the fox than did controls (Fig. 3, Table 2). There was also a significant group \times time interaction in the comparison of vigilance levels with the cat model, reflecting a relatively brief increase in vigilance in the experimental group relative to the control group, even though the wallabies had not seen this model

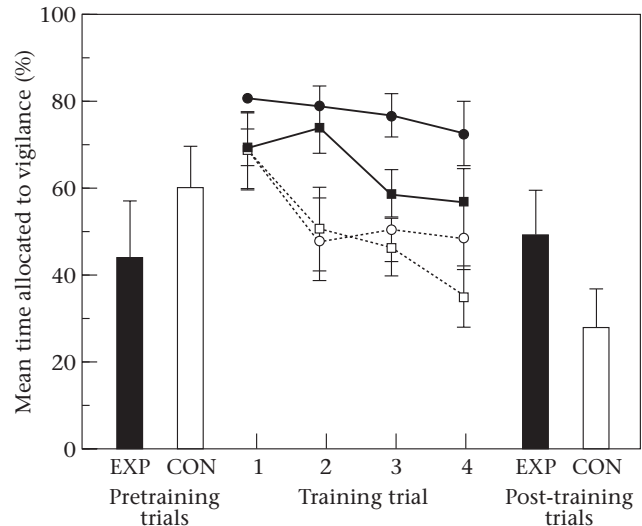


Figure 2. Vigilance behaviour of observer wallabies (■: experimental, $N=8$; □: control, $N=8$) and demonstrator wallabies (●: fox-fearful, $N=4$; ○: fox-indifferent, $N=3$) over the course of the four training trials. Vigilance levels ($\bar{X} \pm \text{SE}$) of experimental (EXP) and control (CON) observers during the pre- and post-training tests in response to the fox are shown for comparison. In some cases, standard errors are smaller than symbols.

during training. In contrast, there were no significant differences between the responses of experimental and control observer wallabies to the goat model, or during blank control trials (Fig. 3, Table 2). These comparisons show that the effect of social training was to inculcate a sustained vigilance response to the fox and a relatively brief one to the cat.

During training, the vigilance behaviour of individual experimental and control observers followed closely that of the demonstrator wallabies with which they were housed, particularly during the first two trials (Fig. 2). Formal analyses revealed a significant positive relation between the demonstrator and observer vigilance levels across the whole training period (Fig. 4). When we examined the relation between the demonstrators' behaviour and that of the observers during the first half and second half of training separately, we found a significant correlation during the first two trials ($r^2=0.229$, $P=0.001$), but not during the second two ($r^2=0.061$, $P=0.141$). The overall level of vigilance decreased in both groups over the course of training (Table 1), particularly in the last two trials (Fig. 2). Taken together, this pattern of results suggests that the effect of the demonstrators' behaviour on that of the observers was strongest initially.

DISCUSSION

Our findings provide the first demonstration of observational conditioning in a marsupial. Antipredator responses previously acquired by the demonstrators through individual training (Griffin et al. 2001) were socially transmitted to predator-naïve wallabies. Wallabies that had watched a fearful demonstrator respond to the fox became more wary of the predator

Table 1. Comparisons between demonstrator groups and observer groups during training

Comparison	ANOVA factor					
	Group		Training trial		Group×Training trial	
	$F_{1,6}$	P	$F_{3,6}$	P	$F_{3,6}$	P
Demonstrators						
Fox-fearful versus fox-indifferent						
Vigilance	23.136	0.002†	2.08	0.204	1.54	0.297
Relaxed behaviour	16.646	0.003†	2.50	0.157	4.06	0.068
Locomotion	9.060	0.012†	5.15	0.043	1.35	0.345
Observers						
Experimental versus control						
Vigilance	2.25	0.185	8.65	0.013	2.01	0.214

Results of two-way (Group×Training trial) repeated measures ANOVAs comparing the mean percentages of time allocated to three behaviours by the two groups of demonstrator wallabies and vigilance levels in the two groups of observer wallabies. All analyses used the Huber and White estimator of variance, which takes into account reduced independence because of reuse of demonstrators. See text for details.

†One-tailed comparison; all others are two tailed.

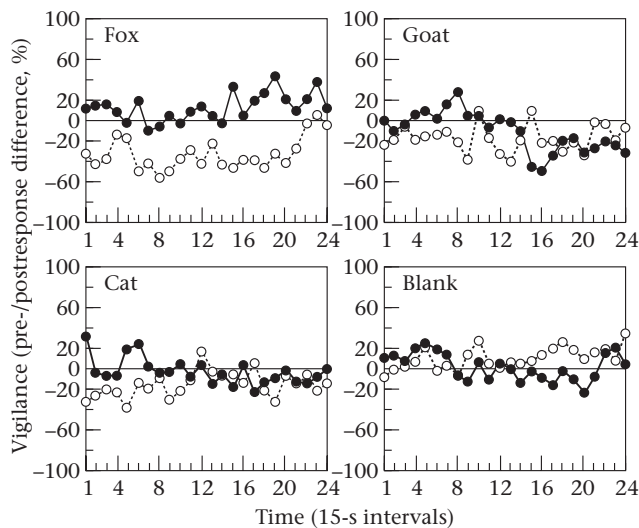


Figure 3. Changes in vigilance after training for the experimental (●, $N=8$) and control observer wallabies (○, $N=8$). The mean pre-/postdifference is plotted for 24 successive 15-s time intervals from stimulus onset. This period includes the stimulus presentation (1 min) and 5 min poststimulus.

model as a consequence. They watched the fox more during presentation and remained vigilant for some minutes afterwards. In contrast, animals in the control group became less wary of the fox after being housed with a social companion that was indifferent to it. There was also evidence of a difference between the two groups in responses to the cat after training, although the period of elevated vigilance in the experimental group was relatively brief. Neither group of wallabies changed their behaviour towards the goat model. Spontaneous behaviour during blank control trials was also unaffected by training. This overall pattern of results shows that observer wallabies attended to the behaviour of demon-

strator conspecifics and that this specifically altered their subsequent responses to the model predators.

In our earlier study (Griffin et al. 2001), in which wallabies were individually trained with a fox model, the effect was to inculcate comparable sustained vigilance responses to both the fox and the cat, even though the latter predator had not been seen during training. In the present study, there is less evidence for stimulus generalization. In particular, differences between experimental and control groups were apparent only as an interaction (Table 2) rather than as a main effect for treatment (cf. Table 1 in Griffin et al. 2001). This informal comparison suggests that the effects of social learning might be more specific than those of individual learning, which could be consistent with other evidence for differences between these two processes (Galef & Durlach 1993).

During training, levels of vigilance in observer wallabies were positively correlated with those of the demonstrator with which they were housed. However, this relation was apparent only during the first half of training, which was also the period in which the highest levels of vigilance were recorded. It seems likely that the tammars learned rapidly, as in other predator recognition studies, which have typically shown that predator avoidance can be acquired in only one to two trials (fish: Magurran 1989; Chivers et al. 1995; birds: Curio 1988; primates: Mineka & Cook 1988).

Both groups of observers watched the fox gradually less over the course of training. This effect was particularly apparent in the experimental group in the last two training trials, suggesting that they began to habituate to the fox model, despite the behaviour of the fox-fearful demonstrators. We suggest that it will be important to explore the way in which the effects of individual learning modulate the expression of antipredator behaviour that has been acquired socially. Studies of food preferences have shown that subsequent individual experience influences whether preferences acquired from

Table 2. Comparisons between experimental and control observer wallabies after training

Comparison	ANOVA factor					
	Group		Time		Group×Time	
	$F_{1,6}$	P	$F_{6,6}$	P	$F_{5,6}$	P
Fox	14.03	0.005†	2.45	0.150	0.67	0.659
Cat	0.87	0.386	0.28	0.925	4.64	0.044
Goat	0.31	0.597	0.12	0.990	0.56	0.730
Blank	0.57	0.477	2.42	0.153	0.50	0.766

Results of two-way (Group×Time) repeated measures ANOVAs comparing the pre/postresponse difference in vigilance levels for each stimulus. All analyses used the Huber and White estimator of variance, which takes into account reduced independence because of reuse of demonstrators. See text for details.

†One-tailed comparison; all others are two tailed.

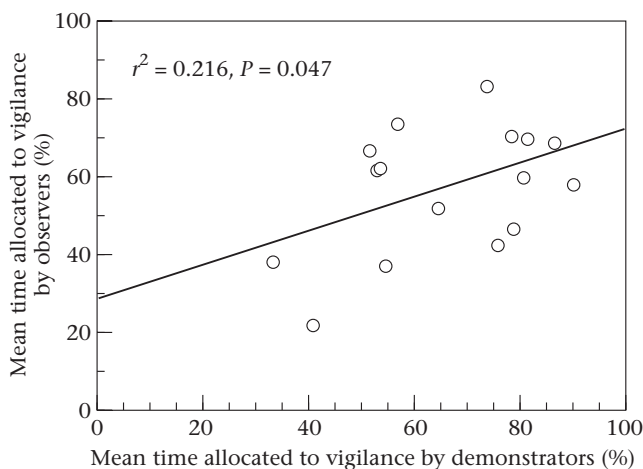


Figure 4. Relation between the mean times allocated to vigilance by the observer and demonstrator wallabies during training.

companions are retained (McQuoid & Galef 1992; Galef & Whiskin 2001). Although it might seem maladaptive for learned predator avoidance not to persist indefinitely, we currently have no basis for predicting how long enhanced responses will be maintained, particularly in free-living animals. Resolution of this issue will require experimental tests, ideally as part of a reintroduction programme.

Our results encourage the training of animals to recognize predators because they raise the possibility that the effects of prerelease training will be maintained by social transmission within a group. This would make predator avoidance training a more cost-effective wildlife management technique. Demonstration of social learning at the individual level is not sufficient to conclude that a behaviour will propagate through an entire population (Galef & Allen 1995), but there is good evidence that diet preferences and predator information can both be transmitted along chains of individuals (Curio et al. 1978; Lefebvre & Palameta 1988; Laland & Plotkin 1990; Galef & Allen 1995) and that this can sometimes lead to stable feeding traditions (Galef & Allen 1995; Reader & Laland 2000) or generate predator-aware populations (Chivers & Smith 1995). Further empirical tests are needed to assess

whether comparable phenomena occur in tammar wallabies.

Social learning has been described in fish, birds and eutherian mammals. The present study provides the first formal demonstration in any species of marsupial. The existence of this phenomenon in a new taxonomic group supports the prediction that social learning is a widespread mechanism for acquiring information about dangerous events (Shettleworth 1998). Our results are more generally the first demonstration of any form of social learning in a marsupial. They suggest that this relatively neglected group has cognitive properties convergent with those of eutherian mammals and encourage comparative studies designed to identify the social and ecological factors responsible.

Acknowledgments

We thank the Fauna Park staff for their assistance in animal management, Linda Evans for comments on the manuscript, Ken Cheng for discussions of experimental design and Alan Taylor for statistical advice. Figure 1 is reproduced with permission from Academic Press. A.S.G. was supported by a Macquarie University International Postgraduate Research Award, the Australian Government Overseas Postgraduate Research Scholarship, the Marsupial CRC and the Swiss Janggen-Pöhn Foundation. C.S.E. was supported by grants from the Australian Research Council and Macquarie University.

References

- Abacus Concepts Inc. 1991. *Superanova*. Berkeley, California: Abacus Concepts.
- Blumstein, D. T., Daniel, J. C., Griffin, A. S. & Evans, C. S. 2000. Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behavioral Ecology*, **11**, 528–535.
- Boyd, R. & Richerson, P. J. 1988. An evolutionary model of social learning: the effects of spatial and temporal variation. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef Jr), pp. 29–47. Hillsdale, New Jersey: L. Erlbaum.

- Brown, C. & Laland, K.** 2001. Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, **59**, 471–493.
- Chivers, D. P. & Smith, R. J. F.** 1995. Free-living fathead minnows rapidly learn to recognize pike as predators. *Journal of Fish Biology*, **46**, 949–954.
- Chivers, D. P., Brown, G. E. & Smith, R. J. F.** 1995. Acquired recognition of chemical stimuli from pike, *Esox lucius*, by brook sticklebacks, *Culaea inconstans* (Osteichthyes, Gasterosteidae). *Ethology*, **99**, 234–242.
- Cook, M., Mineka, S., Wolkenstein, B. & Laitsch, K.** 1985. Observational conditioning of snake fear in unrelated rhesus monkeys. *Journal of Abnormal Psychology*, **94**, 591–610.
- Croft, D. B.** 1989. Social organization of the Macropodoidea. In: *Kangaroos, Wallabies and Rat-kangaroos* (Ed. by G. Grigg, P. Jarman & I. Hume), pp. 505–525. Chipping Norton, New South Wales: Surrey Beatty.
- Curio, E.** 1988. Cultural transmission of enemy recognition by birds. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef, Jr), pp. 75–97. Hillsdale, New Jersey: L. Erlbaum.
- Curio, E., Ernst, U. & Vieth, W.** 1978. The adaptive significance of avian mobbing. II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints. *Zeitschrift für Tierpsychologie*, **48**, 184–202.
- Galef, B. G., Jr & Allen, C.** 1995. A new model system for studying behavioural traditions in animals. *Animal Behaviour*, **50**, 705–717.
- Galef, B. G., Jr & Durlach, P. J.** 1993. Absence of blocking, overshadowing, and latent inhibition in social enhancement of food preferences. *Animal Learning and Behavior*, **21**, 214–220.
- Galef, B. G., Jr & Whiskin, E. E.** 2001. Interaction between social and individual learning in food preferences of Norway rats. *Animal Behaviour*, **62**, 41–46.
- Griffin, A. S., Blumstein, D. T. & Evans, C. S.** 2000. Training captive-bred or translocated animals to avoid predators. *Conservation Biology*, **14**, 1317–1326.
- Griffin, A. S., Evans, C. S. & Blumstein, D. T.** 2001. Learning specificity in acquired predator recognition. *Animal Behaviour*, **62**, 577–589.
- Huber, P. J.** 1967. The behavior of maximum likelihood estimates under non-standard conditions. In: *Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability. Vol. 1*, pp. 221–233. Berkeley, California: University of California Press.
- Klopfer, P. H.** 1961. Observational learning in birds: establishment of behavioural modes. *Behaviour*, **17**, 71–80.
- Laland, K. N. & Plotkin, H. C.** 1990. Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Animal Learning and Behavior*, **18**, 246–251.
- Lefebvre, L. & Palameta, B.** 1988. Mechanisms, ecology and population diffusion of socially-learned food-finding behavior in feral pigeons. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef, Jr), pp. 141–164. Hillsdale, New Jersey: L. Erlbaum.
- Lefebvre, L., Palameta, B. & Hatch, K. K.** 1996. Is group-living associated with social learning? A comparative test of a gregarious and a territorial Columbidae. *Behaviour*, **133**, 241–261.
- McLean, I. G., Hölzer, C. & Strudholme, B. J. S.** 1999. Teaching predator-recognition to a naive bird: implications for management. *Biological Conservation*, **87**, 123–130.
- McLean, I. G., Schmitt, N. T., Jarman, P. J., Duncan, C. & Wynne, C. D. L.** 2000. Learning for life: training marsupials to recognise introduced predators. *Behaviour*, **137**, 1361–1376.
- McQuoid, L. M. & Galef, B. G., Jr.** 1992. Social influences on feeding site selection by Burmese fowl (*Gallus gallus*). *Journal of Comparative Psychology*, **106**, 137–141.
- Magurran, A. E.** 1989. Acquired recognition of predator odour in the European minnow (*Phoxinus phoxinus*). *Ethology*, **82**, 216–223.
- Maxwell, S., Burbidge, A. A. & Morris, K.** (Eds) 1996. *The 1996 Action Plan for Australian Marsupials and Monotremes*. Canberra: National Parks & Wildlife.
- Mineka, S. & Cook, M.** 1988. Social learning and the acquisition of snake fear in monkeys. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef, Jr), pp. 51–73. Hillsdale, New Jersey: L. Erlbaum.
- Noldus Information Technologies** 1995. *The Observer 3.0*. Wageningen, The Netherlands: Noldus Information Technologies.
- Reader, S. M. & Laland, K. N.** 2000. Diffusion of foraging innovations in the guppy. *Animal Behaviour*, **60**, 175–180.
- SAS Institute** 1998. *Statview 5.0*. Cary, North Carolina: SAS Institute.
- Shettleworth, S. J.** 1998. *Cognition, Evolution, and Behavior*. New York: Oxford University Press.
- Short, J., Bradshaw, S. D., Giles, J., Prince, R. I. T. & Wilson, G. R.** 1992. Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia: a review. *Biological Conservation*, **62**, 189–204.
- Springer, M. S., Westerman, M. & Kirsch, J. A. W.** 1994. Relationships among orders and families of marsupials based on 12S ribosomal DNA sequences and the timing of the marsupial radiation. *Journal of Mammalian Evolution*, **2**, 85–115.
- StataCorp** 1999. *Stata Statistical Software: release 6.0*. College Station, Texas: Stata Corporation.
- Suboski, M. D.** 1990. Releaser-induced recognition learning. *Psychological Review*, **97**, 271–284.
- White, H.** 1980. A heteroskedasticity-consistent covariance matrix estimator and a direct test for heteroskedasticity. *Econometrica*, **48**, 817–830.
- White, H.** 1982. Maximum likelihood estimation of misspecified models. *Econometrica*, **50**, 1–25.