

Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators

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We studied the way in which a population of tammar wallabies (*Macropus eugenii*), which have been isolated from mammalian predators since the last ice age, responded to the sight and sound of historical and ontogenetically and evolutionarily novel predators. Tammar wallabies were shown a range of visual stimuli, including taxidermic mounts of two evolutionarily novel predators, a red fox (*Vulpes vulpes*) and a cat (*Felis catus*), and a model of an extinct predator, the thylacine (*Thylacinus cynocephalus*). Controls were a conspecific, the cart on which all mounts were presented, and blank trials in which spontaneous change in behavior was measured. We played back recorded sounds to characterize responses to acoustic cues from predators and to a putative conspecific antipredator signal. Treatments included the howls of dingoes (*Canis lupus dingo*), an evolutionarily novel predator; calls of a wedge-tailed eagle (*Aquila audax*), a historical and current predator; and wallaby foot thumps. Controls were the song of an Australian magpie (*Gymnorhina tibicen*) and a blank trial. After seeing a fox, wallabies thumped their hind feet in alarm, suppressed foraging, and increased looking. The sight of a cat similarly suppressed foraging and increased looking. The sounds of predators did not influence responsiveness, but wallabies foraged less and looked more after thump playbacks. Our results suggest that tammar wallabies respond to the sight, but not the sounds, of predators. In contrast, the response to foot thumps demonstrates that this particular sound functions as an antipredator signal. We suggest that responsiveness to visual cues has been preserved under relaxed selection because predator morphology is convergent, but vocalizations are not. *Key words*: antipredator behavior, *Macropus eugenii*, predator recognition, relaxed selection, tammar wallaby. [*Behav Ecol* 11:528–535 (2000)]

The degree to which antipredator behavior persists or is lost under relaxed selection is of considerable theoretical interest (Byers, 1997; Coss, 1991, 1999; Magurran, 1999), and it also has practical implications for the conservation and management of geographically isolated populations (Berger, 1998, 1999). In some cases, species that do not encounter predators for many generations lose their ability to respond to them. This evolutionary isolation may be natural, as might occur on an island isolated from the mainland, or in other predator-free habitat patches (Curio, 1966, 1975; Kavaliers, 1990; Levesley and Magurran, 1988; Seghers, 1974). Alternatively, isolation may result from human-induced habitat fragmentation or population management (Berger, 1998). Antipredator behavior is not inevitably lost under such circumstances; some species retain effective responses to predators after long periods of isolation. The factors responsible for retention are a topic of considerable interest (Coss, 1999; Curio, 1966; Pressley, 1981). For instance, species might lose a specific response evoked by a particular predator, while retaining more general antipredator behavior evoked by cues that are shared by several predators. In this study, we quantified the way in which individuals from a population isolated from some predators since the last ice age responded to the sights and sounds of both historical and evolutionarily novel predators. We wanted to determine whether responsiveness is retained under relaxed selection and also whether it can be generalized to novel predators.

In principle, prey may respond to cues associated with predators in any sensory modality. In the present study we concentrated on the effects of visual and acoustic stimuli generated by predators and also characterized the response evoked by a putative acoustic antipredator signal, the foot thump (Coulson, 1996). Visual predator recognition sometimes depends on simple cues, such as apparent size, shape, speed, or the presence of frontally positioned eyes (e.g., Coss and Goldthwaite, 1995; Curio, 1993; Evans et al., 1993; Tinbergen, 1951). These features are typically common to a class of predators (e.g., carnivores have binocular vision and positioned eyes; attacking raptors fly quickly) and thus permit potential prey to respond both to historical predators and to evolutionarily novel ones (but see Hirsch and Bolles, 1980).

Acoustic predator recognition may be different. While hunting, predators are typically quiet and stealthy, but they must also communicate with conspecifics (e.g., Schaller, 1972). These social signals reveal the presence of a predator and could be exploited by omniscient prey to enhance vigilance. In fact, antipredator behavior is reliably elicited by the sounds produced by some species' predators (Hauser and Wrangham, 1990; Hendrie et al., 1998; Macedonia and Yount, 1991; Noë and Bshary, 1997; Swaisgood et al., 1999; Zuberbühler et al., 1997). Among predators, selection for species identification leads to divergent signal structure (e.g., the territorial vocalizations of related canids are structurally distinct; Estes, 1991). Consequently, acoustic recognition of predators will depend on relatively specific cues. We might thus expect species to be less able to respond to the sounds of evolutionarily and ontogenetically novel predators than to those of historically important ones.

In summary, selection for optimal hunting will produce convergent morphology, while the constraints of effective communication will produce divergent sounds. We might

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therefore expect species to respond to the sights, but not the sounds, of evolutionarily novel predators.

In Australia, many small-bodied marsupials face extinction from predation by red foxes introduced by Europeans in the last century (Coman, 1995). Initially, this detrimental impact of a novel predator may seem surprising because Australia historically had a rich community of marsupial carnivores, including lions (Thylacoleonidae), wolves (Thylacinidae), cats, and hyenas (Dasyuridae) (Archer, 1981; Robertshaw and Harden, 1989; Wroe, 1999). Today many species or populations survive only on predator-free offshore islands (Johnson et al., 1989). We studied one of these isolated populations, tammam wallabies (*Macropus eugenii*) from Kangaroo Island, South Australia.

Tammars are a mid-sized (4–7 kg), moderately social wallabies found in several geographically isolated and genetically distinct populations with different histories of exposure to mammalian predators (Cooper and McKenzie, 1997; Croft, 1989; Smith and Hinds, 1995). Although they evolved with marsupial predators that preyed on tammam-sized wallabies (e.g., Jones and Stoddard, 1998), tammars on Kangaroo Island have not typically been exposed to mammalian predators since the island's isolation from the mainland about 9500 years ago (Lampert, 1979). The only substantial mammalian predator on Kangaroo Island, the Tasmanian devil (*Sarcophilus harrisi*), is known only from the fossil record (Pledge, 1979). Devils are not effective predators on healthy, wallaby-sized animals (Buchmann and Guiler 1977; Jones, 1995; but see Jones, 1994). There are no records of the now extinct thylacine (*Thylacinus cynocephalus*), dingoes (*Canis lupus dingo*), or red foxes (*Vulpes vulpes*) having ever lived on the island. A small, low-density population of feral cats (*Felis catus*) introduced in the last century, as well as domestic farm dogs (*Canis familiaris*), are found around human settlements, the majority of which are restricted to the eastern part of the island. A diurnal raptor, the wedge-tailed eagle (*Aquila audax*), is a current, and presumably historical, resident of Kangaroo Island that may prey on tammars. Kangaroo Island tammars are thus ideally suited for study of the responses to both evolutionarily novel and historically important predators.

METHODS

Subjects and husbandry

We selected 19 adult tammam wallabies (16 females, 3 males) from a breeding colony maintained at the Macquarie University Fauna Park, Sydney, Australia. When not participating in the experiment, the wallabies lived in female-biased, mixed-sex aggregations. Subjects were either wild caught or captive bred from Kangaroo Island stock. Wild-caught subjects had lived in the Fauna Park for >2 years. For this study, we temporarily isolated each experimental subject in one of four 4 × 12 m fenced enclosures. The fences of each enclosure were covered with a 2 m high band of an opaque, black, woven synthetic fabric (weedmat) with an observation window cut into one of the small ends. Subjects were thus visually isolated from most movements outside the enclosure, but they could see the head and shoulders of the observer. The experimental enclosures contained shelter (arranged so as not to interfere with our vision) and ad libitum water. We provided food in a central location two times per day. An opening on each side of the enclosure revealed a stage on which a visual stimulus appeared, or beside which a speaker was hidden.

Stimulus conditions and justification

We selected a range of predator stimuli to include both a prototypical historical predator and evolutionarily novel intro-

duced predators. Wallaby responses were compared to those evoked by control nonpredator stimuli and blank trials in which no stimulus was presented. In addition, we studied the response to a putative acoustic antipredator signal.

We exposed tammars to six visual treatments. Three predatory stimuli were chosen based on the pattern of evolutionary and ontogenetic isolation. A model thylacine, made of injection molded foam, was ontogenetically novel, but was a potentially important historical predator with which tammars should have had evolutionary experience. A cat was chosen because it was possibly ontogenetically familiar (feral and domestic cats sometimes wandered through the Fauna Park) but evolutionarily novel. A fox was both ontogenetically and evolutionarily novel. We also presented a taxidermically mounted wallaby to quantify the response to a nonpredatory, familiar vertebrate. We had two further controls. A cart control allowed us to quantify the response to the presentation device and its associated movement without a vertebrate stimulus, and a blank control allowed us to measure spontaneous behavioral change in the absence of a stimulus presentation.

We exposed tammars to five acoustic treatments. Tammam foot thumps were played back to document response to a putative antipredator signal. We used the calls from a wedge-tailed eagle to represent acoustic cues from a historical and current predator. Similarly, the howls recorded from a pack of dingoes represent both an ontogenetically and evolutionarily novel predator-generated sound. We chose dingoes because they are more vocal than foxes. The remaining two conditions were controls. Playback of the song of an Australian magpie (*Gymnorhina tibicen*) allowed us to quantify the response to an ontogenetically and evolutionarily familiar nonpredator that often sings from the ground. As in the visual treatments, a blank control allowed us to measure spontaneous behavioral change.

Experimental protocol

Subjects were removed from their normal enclosures and habituated to the experimental setup for 3 days before the experiment began. Tammars were fed half their daily allotment of food (kangaroo pellets and rolled oats) in the morning (within 3 h of sunrise) and half in the late afternoon (within 3 h of sunset). This provisioning schedule corresponded with the times at which experiments were subsequently conducted. Tammars, although primarily nocturnal, are active in the mornings and in the late afternoon (Blumstein et al., 1999). In nature, tammars begin to move from their day bed to communal foraging grounds in the late afternoon and return to their day bed by the early morning. Thus, these times approximate when tammars naturally move through their habitat and would be most likely to encounter predators.

On the morning of the fourth day, and for the next six mornings, we exposed subjects to one of five visual stimuli or the blank control (Figure 1). Each stimulus was presented on a cart which ran along a wooden or aluminium track and appeared in the window, where it remained for 60 s before being pulled away.

On the afternoon of the fourth day and for the next five afternoons, we exposed subjects to one of four acoustic stimuli or the blank control (Figure 2). We used two exemplars of each stimulus to sample natural variation in acoustic structure. Dingo howls and wallaby thumps were recorded using a Sennheiser ME-67 microphone with a Sony TCD-5M cassette recorder. The wedge-tailed eagle recordings were obtained from a commercial recording (Buckingham and Jackson, 1985), and the magpie recordings were obtained from a private collection. All sounds were digitized (Digidesign Audiomedia II A/D board, Pro Tools software, sample rate 44.1

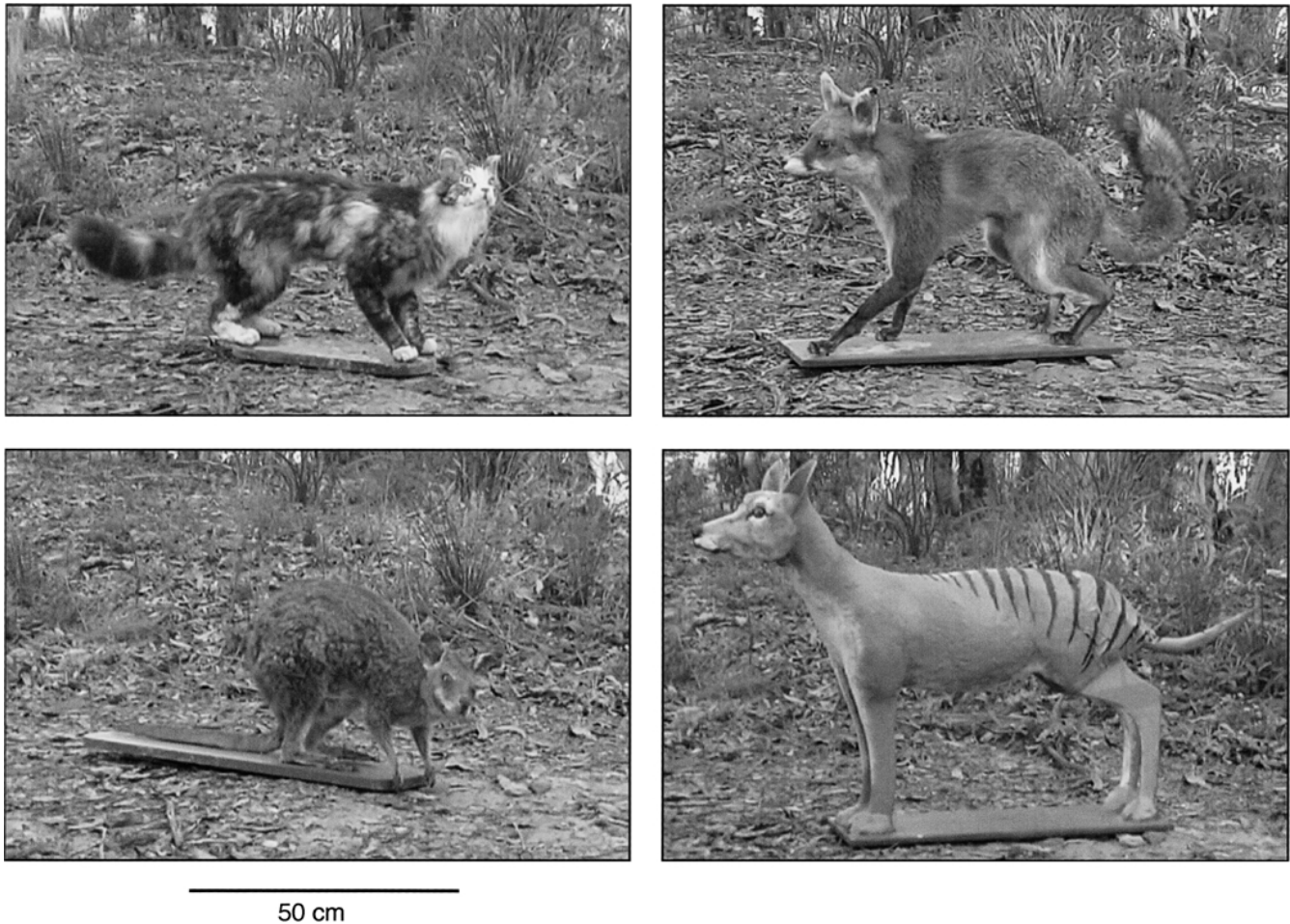


Figure 1

Visual stimuli used to study tammar wallaby predator recognition. Clockwise from upper left: cat, red fox, model thylacine, tammar wallaby.

kHz, 16-bit amplitude encoding), edited to create a 4–5 s acoustic stimulus, and down-sampled to 8 bits for playback using a PowerBook 100 computer through a Sony SRS-77G powered speaker. Our playbacks were designed to mimic the sound of an adjacent wallaby foot-thumping, a nearby eagle, a more distant group of howling dingoes, and a nearby singing magpie. Thumps were played back at an amplitude of 82 dB (A weighting; peak; ± 1 dB measured 1 m in front of the speaker); the other three stimuli were played back at 92 dB (± 1 dB).

Our goal was to present stimuli to subjects foraging in the center of the test enclosure to control for behavior, motivational state, and location. Pilot trials demonstrated that food type influenced vigilance patterns: wallabies eating only rolled oats had extended bouts of foraging with their nose held close to the ground. We climbed through the observation window and placed a handful of rolled oats at a predetermined central location 2–3 m from the window where the visual stimulus would appear or from the location of the hidden speaker. However, animals did not always feed when we set up a test trial. Some individuals rested or slept in the back of the enclosure, while others appeared to wait nervously for us to leave. Pilot trials demonstrated that wallabies that did not begin feeding within 15 min were not motivated to feed, so we waited a maximum of 30 min before presenting the stimulus. An additional criterion for visual stimuli was that subjects had to have an unobstructed view of the stage.

Stimuli were presented in a within-subjects repeated-measures design. Each subject was exposed to each stimulus once.

To reduce the likelihood of habituation to our stimuli and to control for order effects, we tested enclosures in a random order, presented all stimuli and controls in a randomly generated but balanced order, and systematically varied the side of the test enclosure in which a stimulus appeared.

Data analysis

Subjects were videorecorded for 1 min before stimulus presentation, 1 min during stimulus presentation, and for 3 min after stimulus presentation. A single observer (J.C.D.) scored the videotapes to 0.1 s resolution using The Observer 3.0 (Noldus Information Technologies, 1995). We calculated the percentage of time allocated to the three most common behaviors [foraging, looking, and pentapedal locomotion (macropods use their tail when walking slowly; in this context, we interpret such pentapedal locomotion as an exploratory behavior)]. Foraging was defined to include both bipedal and quadrupedal foraging. Heightened looking was characterized by standing upright or rearing up on hind legs. In all cases, we used the 1 min preceding stimulus presentation as a baseline from which we calculated the difference in time allocation following stimulus presentation. One way repeated-measures ANOVAs for each behavior revealed no significant differences during the baseline period (visual treatments: foraging, $p = .60$, looking, $p = .65$, pentapedal locomotion, $p =$

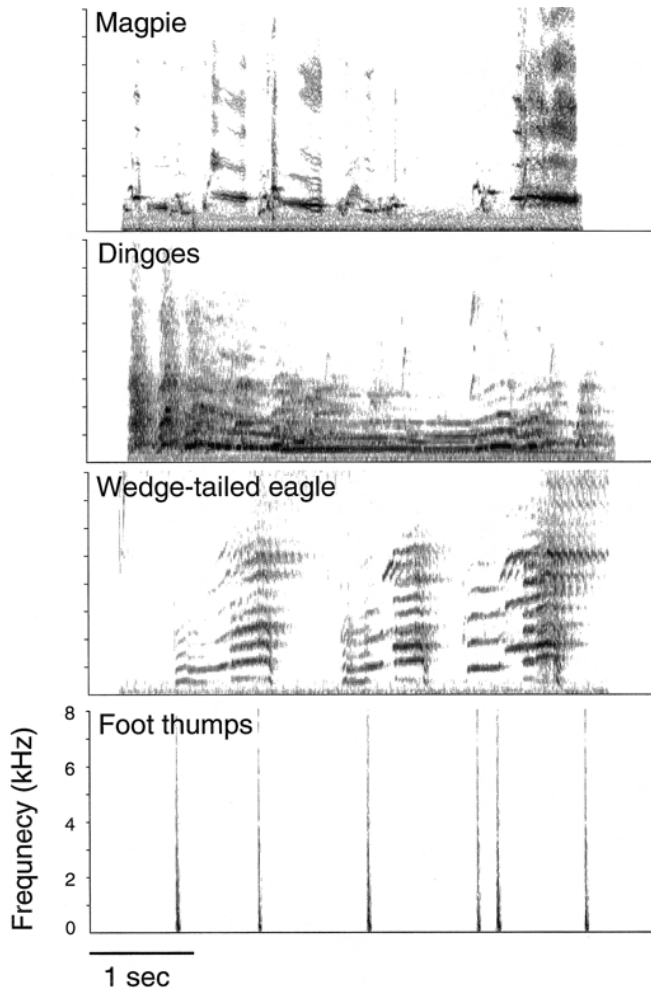


Figure 2
Spectrograms of one of the two exemplars of acoustic stimuli used to study tamar wallaby predator recognition. Sampling rate 44.1 kHz, 512 point FFT (frequency resolution 350 Hz), gray scale represents -40 dB from peak amplitude).

.15; acoustic treatments: foraging, $p = .57$; looking, $p = .95$; pentapedal locomotion, $p = .46$).

Responses to the visual and acoustic stimuli were relatively transient. To quantify these changes in behavior, we examined time allocation in successive 15-s intervals, beginning at stimulus onset. For the visual treatments, we ignored the first 15 sec interval because all stimuli elicited a marked, but ephemeral, orienting response, and focused instead on the three 15-s intervals while the stimulus was present and stationary. We wanted to identify change in behavior due to the stimulus, independent of baseline rates, so we calculated the difference between baseline time allocation and that in each of the three 15-s intervals and modeled variation in time allocated to foraging, looking, and walking with a two-factor repeated-measures ANOVA. Some individuals also foot thumped in response to presentations of visual stimuli. We tested for a relationship between the probability of thumping and stimulus type using a Cochran's Q test, followed up by post-hoc pairwise McNemear's tests.

Responses to the 4 to 5-s acoustic stimulus presentation were very brief. We thus focused only on the 15-s interval that began with the playback. As with visual treatments, we calculated the difference between the percent baseline time allocation and that during the 15-s poststimulus interval and then

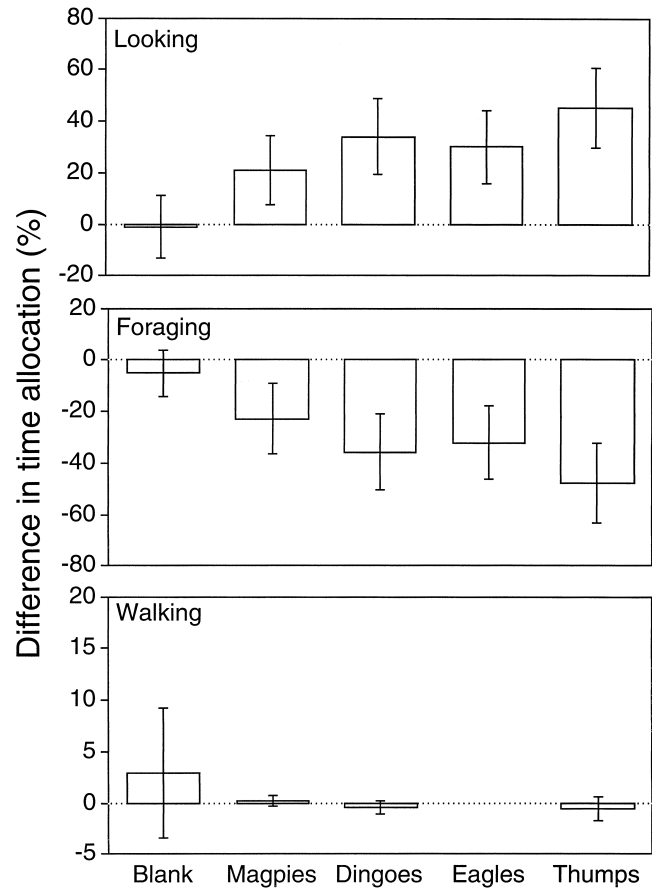


Figure 3
Average percent difference ($\pm 95\%$ CI) in time allocated to looking, foraging, and walking in the final 45 s of a 60-s visual stimulus presentation compared to baseline. Note that scales differ to facilitate comparison within a dependent measure.

fitted one-factor repeated-measures ANOVA models to explain variation in foraging, looking, and walking.

Statistical and power analyses were conducted using Statview 5.0 (SAS Institute, 1998), SuperAnova 1.1 (Abacus Concepts Inc., 1991), and G*Power (Buchner et al., 1996). Significance was set at $p < .05$. We visually examined residuals from parametric models; these appeared to be normally distributed. For repeated-measures ANOVAs, we report the Huynh-Feldt corrected p values. For subsequent planned pairwise comparisons, we report Huynh-Feldt corrected p values unadjusted for multiple comparisons (Carmer and Swanson, 1973). We also conducted post-hoc power analyses to estimate the sample size required to differentiate key negative results with 70% power.

RESULTS

Visual treatments

Tamar wallabies responded to the presentation of all quadrupedal stimuli, particularly the cat and fox (Figure 3). Overall, foraging was inhibited, and both looking and locomotion were enhanced (foraging main effect: $F_{5,90} = 3.87$, $p = .004$; looking main effect: $F_{5,90} = 3.03$, $p = .027$; locomotion main effect: $F_{5,90} = 3.32$, $p = .017$). There was also a significant interaction between treatment and time for foraging ($F_{10, 180} = 3.690$, $p = .0006$) but not for the other behaviors (looking: $F_{10, 180} = 1.867$, $p = .074$; locomotion: $F_{10, 180} = .879$, $p = .540$).

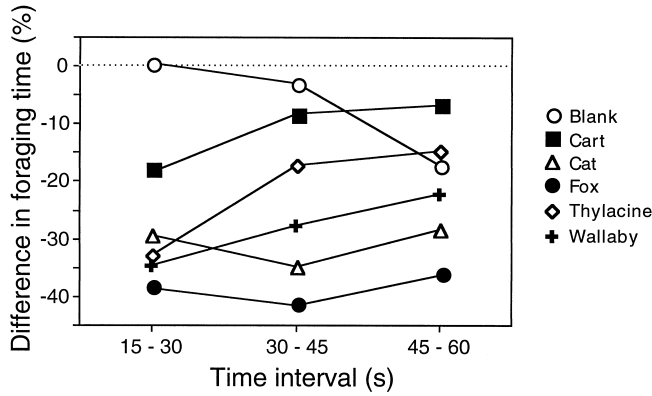


Figure 4
The percent difference in time allocated to foraging showing the interaction between time since initial stimulus presentation and stimulus type.

There were no significant main effects of time (largest $F_{2,36} = 1.58, p = .225$).

We first compare the treatments by considering significant main effects. The fox significantly suppressed foraging relative to the cart ($F_{1,90} = 9.871, p = .003$) and blank ($F_{1,90} = 13.416, p = .0005$). Presentations of the fox also enhanced looking relative to the cart ($F_{1,90} = 9.657, p = .006$) and blank ($F_{1,90} = 9.630, p = .006$). Tammars responded similarly to the cat, which also suppressed foraging and enhanced looking (foraging: cat versus cart, $F_{1,90} = 4.996, p = .029$; cat versus blank, $F_{1,90} = 7.596, p = .008$; looking: cat versus cart, $F_{1,90} = 4.719, p = .044$; cat versus blank, $F_{1,90} = 4.701, p = .044$). Wallaby presentation also suppressed foraging (wallaby versus blank $F_{1,90} = 5.994, p = .017$). Locomotion too, was influenced by stimulus type. Tammars walked significantly more after seeing the fox and wallaby compared to the cart (fox, $F_{1,90} = 8.070, p = .010$; wallaby, $F_{1,90} = 5.773, p = .027$) and blank control (fox, $F_{1,90} = 10.510, p = .004$; wallaby, $F_{1,90} = 7.861, p = .011$).

We now consider the significant interaction between stimulus and time for foraging. The overall pattern was that subjects suppressed foraging most during fox and cat presentations (Figure 4). Subjects suppressed foraging significantly more after seeing the fox ($F_{2,36} = 4.206, p = .028$) and the cat ($F_{2,36} = 4.486, p = .018$) compared to the thylacine. Animals presented with no stimulus (the blank control) tended to forage less over time, illustrating an expected regression to the mean for this condition. There were significant stimulus \times time interactions in all comparisons between the blank control and other treatments, which were each characterized by increased foraging over time (smallest $F_{2,36} = 3.599, p < .038$).

Post hoc power analyses emphasized the variation intrinsic in these response variables. For looking, we would have needed a median sample size of 148 subjects to better differentiate the nonsignificant responses to the stimuli (range = 30 for the wallaby-cart contrast to 388 for the wallaby-thylacine contrast). Similarly, for foraging, we would have needed a median sample size of 105 subjects to better differentiate the nonsignificant responses to the stimuli (range = 30 for the wallaby-cart contrast to 1420 for the wallaby-cat contrast). For walking, we would have needed a median sample size of 107 subjects to better differentiate the nonsignificant responses to the stimuli (range = 34 for the cart-thylacine contrast to 3350 for the cat-thylacine contrast).

The probability of tammars thumping varied significantly across our six visual test conditions (Table 1; Cochran's $Q = 18.8, p = .002$). Subjects were more likely to thump after seeing a fox than controls (McNemear's $p = .004$ for blank, $p =$

Table 1

The number of individuals that alarm thumped in response to the presentation of visual stimuli

	Thumped ^a
Blank	0
Cart	1
Wallaby	3
Thylacine	4
Cat	4
Fox	9

Each of 19 subjects were exposed in a random order to all six stimuli.

^a Cochran's $Q = 18.8, p = .002$.

.022 for cart, $p = .031$ for wallaby). However, a more conservative post hoc analysis using a sequential Bonferonni test (Rice, 1989) suggests that subjects were only significantly more likely to thump in response to the fox than to the blank control.

Acoustic treatments

Wallabies responded to hearing sounds by foraging less and looking more (Figure 5). This was reflected by significant

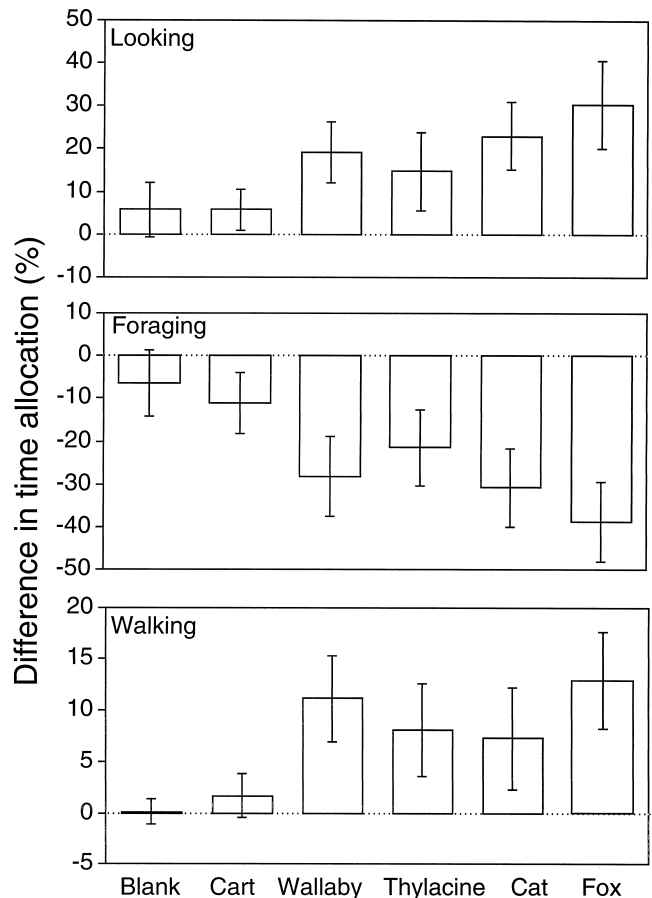


Figure 5
Average percent difference ($\pm 95\%$ CI) in time allocated to looking, foraging, and walking in the 15 s during and after acoustic stimulus presentation compared to baseline. Note that scales differ to facilitate comparison within a dependent measure.

Table 2
Summary of significant pairwise comparisons of tammars' responses to visual stimuli

	Main effect			Elicited thumps
	Foraging	Looking	Walking	
Fox	B, C	B, C	B, C	B, C, W
Cat	B, C	B, C		
Thylacine				
Wallaby	B		B, C	

B = blank, C = cart, W = wallaby.

ANOVA main effects for foraging ($F_{4,72} = 5.920$, $p = .0004$) and looking ($F_{4,72} = 5.309$, $p = .0008$), but not locomotion ($F_{4,72} = 1.103$, $p = .313$).

Playback of thumps elicited significantly greater responses than both the blank control and the magpie control (foraging smaller $F_{1,72} = 7.276$, $p = .009$; looking smaller $F_{1,72} = 6.230$, $p = .015$). In contrast, the effects of predator sounds (dingoes and eagle) were not significantly different from those of the magpie song, but they each differed from the blank control (foraging: smaller $F_{1,72} = 8.559$, $p = .005$; looking: smaller $F_{1,72} = 5.399$, $p = .023$). The magpie control, however, did not significantly change behavior relative to the blank.

Post hoc power analyses again emphasized the level of variability in evoked responses. For looking, we would have needed a median sample size of 95 subjects (range = 27 for the magpie–eagle contrast to 292 for the dingo–magpie contrast) to better differentiate the nonsignificant responses to the different stimuli. Similarly, for foraging, we would have needed a median sample size of 85 subjects (range = 50 for the thumps–eagle contrast to 900 for the dingo–eagle contrast) to better differentiate nonsignificant responses.

DISCUSSION

The overall pattern of our results (Table 2) suggests that Kangaroo Island tamar wallabies respond to the sight of both evolutionarily and ontogenetically novel predators. The fox and cat stimuli inhibited foraging and enhanced vigilance relative to the cart and blank controls. Both the fox and the wallaby control stimulus increased pentapedal locomotion. Analysis of foot thumps, which we interpret as the highest level of antipredator behavior, revealed that the fox uniquely elicited more thumps than all three control stimuli. In contrast, the model thylacine, a species with which tammars shared a long evolutionary history (but for which a taxidermic mount was unavailable), did not elicit higher levels of response than the taxidermic mounts of novel predators.

The sounds of historical and novel predators did not modify tamar time allocation, nor did they elicit foot thumps. However, tammars did respond to playback of foot thumps by decreasing foraging and increasing vigilance (Figure 5). This response could result from continued exposure to thumps which are elicited by people walking through the Fauna Park. To our knowledge, this is the first demonstration that the almost ubiquitous macropod foot thump functions as a conspecific antipredator signal. Coulson (1996) examined the situation in which foot thumps were produced and concluded that for Western grey kangaroos (*Macropus fuliginosus*), foot thumps may function to deter pursuit from predators (Hasson, 1991). Alarm signals can have multiple targets and multiple functions (Blumstein and Armitage, 1998; Evans 1997), so these are not mutually exclusive interpretations. Thus, although tammars were unresponsive to sounds produced by

predators, they remain sensitive to the alarm signals of conspecifics.

Taken together, these results suggest that Kangaroo Island tamar wallabies continue to respond to the sight of predators despite 9500 years of evolutionary isolation. These results are consistent with predictions about the generalizability of visual cues, in contrast with the diverse and species-specific nature of acoustic cues. Our study was designed to document the responses evoked by prototypical exemplars of historical and current predators. Future experiments would be required to identify the specific visual features (e.g., frontally positioned eyes, size, shape, body posture) that enabled tammars to respond to novel predators. Such experiments might also reveal why our thylacine model was deficient.

We suggest that recognition of visual features that are widely shared among predators may be more likely to persist despite relaxed selection than recognition of idiosyncratic acoustic cues. Such differences may also reflect the relative importance of ontogeny, or very recent selection on Kangaroo Island for responses to cats and dogs. It is possible, although unlikely, that some of our subjects were exposed to cats and dogs before capture. Although prey may be more likely initially to respond to visual cues from novel predators than to their sounds, they still may be able to learn predator vocalizations. Macedonia and Yount (1991) found that a captive colony of lemurs (*Lemur catta*) learned the calls of the evolutionarily novel aerial predators present in their seminatural captive environment. We know that tammars at the Macquarie Fauna Park heard foot-thumps on a daily basis, but we do not have the detailed knowledge of prior exposure to wedge-tailed eagle calls that would allow us to assess the importance of learning for responsiveness to acoustic stimuli.

It is possible that olfactory cues associated with the taxidermic mounts explained some variation in the tammars' response. We are currently studying olfactory predator recognition. If olfactory cues were important, then we would expect also to find differences between treatments in time allocation before stimulus presentation, when the mounts were in position adjacent to the stage. However, there were no differences in baseline time allocation, suggesting that subjects did not respond to the smell of the fox or cat before they saw either stimulus.

There is substantial variation in the response of prey species to a period of relaxed selection. Berger (1998) found a decrease in predator recognition abilities of North American ungulates isolated from predators for only 50–100 years. In contrast, Byers (1997) noted that the antipredator behavior of pronghorn (*Antilocapra americana*) has persisted, despite the extinction during the last ice age of the predators with which they evolved. Similarly, Coss (1999) found that ground squirrels isolated from predators for 70,000–300,000 years have retained predator recognition abilities.

What is it about isolation that influences the likelihood of a trait persisting over time? Coss (1999) suggested that functionally integrated behaviors will likely persist over time. He argued that, although there may be selection against a costly antipredator behavior system, selection for components that are functional in other contexts may be sufficient to maintain antipredator behavior. Avoidance responses involved in antipredator behavior may have an underlying physiological response shared with another system (e.g., social behavior). Thus, selection in the other context may be sufficient to maintain antipredator behavior in the absence of direct selection. Similarly, the continued presence of one class of predators (e.g., raptors) may maintain functionally linked antipredator responses to another class (e.g., carnivores; Blumstein and Daniel, unpublished data). Finally, the cost of antipredator behavior must be considered. If responding to the sight of a

potential predator imposes no substantial energetic or life-history costs, then a geographically isolated population will experience no costly false positive identifications and may effectively have no cost to maintaining some degree of responsiveness (Magurran, 1999; van Damme and Castilla, 1996).

Although tammars responded to the sight of a fox, which was an entirely novel predator, changes in locomotor behavior were limited and baseline behavior was resumed within 2 min after presentations. Many species of macropods are endangered on mainland Australia, where their populations have been decimated by introduced red foxes. There has been considerable recent interest in prerelease training of endangered species to enhance their responses to predators (Griffin et al., in press; McLean et al., 1994, 1999). Knowing how and when to allocate scarce resources to prerelease predator training programs is vitally important. We have suggested that training will be most successful for those species that already possess rudimentary antipredator behavior (Griffin et al., in press). Results from the present study are encouraging because they demonstrate that tammars retain the ability to respond to visual cues associated with predators, despite a long period of isolation. We suggest that prerelease predator training is likely to be successful for tammar wallabies, and potentially for other endangered macropods, because even evolutionarily isolated populations continue to respond to the sight of predators.

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