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A Test of the Multi-Predator Hypothesis: Rapid Loss of Antipredator Behavior after 130 years of Isolation

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Abstract

Many species find themselves isolated from the predators with which they evolved. Isolation often leads to the loss of costly antipredator behavior, which may have adverse consequences if the population should later come into contact with predators. An understanding of both the mechanism (i.e. the degree to which antipredator behavior depends on experience), and of the time course of loss is important to be able to predict how a population will respond to future contact. We studied 'group-size effects' – the way in which animals change the time they allocate to antipredator vigilance as a function of group size – and visual and acoustic predator recognition in a population of tammar wallabies (*Macropus eugenii*), a cat-sized (6–10 kg) macropodid marsupial. To study group size effects we observed wallabies foraging in four populations – three with some sort of predator and a New Zealand population that was isolated from all predators for about 130 yr. To study predator recognition, we observed the response of New Zealand wallabies to the presentation of a model or taxidermic mount of mammalian predators, and to the broadcast sounds of mammalian and avian predators. We compare these predator recognition experiments with results from a previous study of Kangaroo Island (South Australia) tammars. Complete isolation from all predators for as few as 130 yr led to the loss of group size effects and a rapid breakdown in visual predator recognition abilities. Our results are consistent with a key prediction of the multi-predator hypothesis – namely, that the isolation from all predators may lead to a rapid loss of antipredator behavior.

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Introduction

The way in which a population's antipredator behavior is modified when animals are isolated from predators depends on its underlying developmental mechanisms (e.g. Blumstein 2000, 2002; Berger et al. 2001). The proper performance of antipredator behavior may require both a heritable predisposition (Riechert & Hedrick 1990) as well as experience (Magurran 1990; Brown et al. 1997). We operationally define experience-dependent antipredator behavior as that which depends on experience with predators (Brown et al. 1997), or with the experience of the conspecifics responding to predators (Curio 1993). Experience-dependent behavior may be lost after the first generation of isolation. In contrast, more 'hard-wired' antipredator behavior may persist for tens to hundreds of thousands of years following isolation (Byers 1997; Coss 1999).

Understanding the time course of this response is of theoretical interest (Coss 1991, 1999; Byers 1997; Magurran 1999; Blumstein et al. 2000; Blumstein & Daniel 2002), and also has practical implications for the conservation and management of geographically isolated populations (Berger 1998, 1999). Experience-dependent behavior may be quickly 'restored' the first time individuals encounter predators (Brown et al. 1997), or via pre-release training (Griffin et al. 2000). In contrast, the loss of more hard-wired behavior may be permanent (Griffin et al. 2000). In this study, we focused on two antipredator behaviors – group size effects and predator recognition abilities – to quantify antipredator behavior in a population isolated from all predators.

Group size effects are the way in which animals modify their time allocation as a function of group size (Bednekoff & Lima 1998). A commonly reported benefit of aggregation is seen when individuals decrease the time devoted to vigilance and increase the time to foraging as group size increases (Lima & Dill 1990). Group size effects should, like many other behavioral traits, be sensitive to the overall level of predation risk. Costly antipredator behavior should not persist once there is no net benefit. Previous research on group size effects has not formally evaluated how it varies with predation risk, nor with how group size effects vary with different types of predation risk (but see Catterall et al. 1992; Blumstein & Daniel 2002).

We also focused on predator recognition abilities because identifying predators is a pre-requisite for efficient escape. We quantified the way in which individuals, from a species already shown to have some degree of hard-wired predator recognition abilities (see below and Blumstein et al. 2000), responded to 130 yr of virtually complete isolation from predators.

We focused on tammar wallabies (*Macropus eugenii*), a mid-sized (maximum female mass = 6 kg; maximum male mass = 10 kg), moderately social macropodid marsupial found naturally in Western Australia, and on several islands off mainland Australia (Smith & Hinds 1995). Individuals from a now-extinct mainland South Australian population were introduced to Kawau Island, New Zealand, about 130 yr ago and were subsequently translocated to the Rotorua area of the North Island (Warburton & Sadleir 1990; Taylor & Cooper 1999). Animals on the South Australian mainland had a rich evolutionary history of exposure to both native predators (marsupial lions, Thylacoleoindae; marsupial tigers/wolves, Thylacinidae; marsupial cats and hyenas, Dasyuridae; as well as large lizards and raptors – Archer 1981; Robertshaw & Harden 1989; Wroe 1999), and introduced predators (dingoes, *Canis lupus dingo*, were introduced to Australia about 3500 yr ago – Corbett 1995; Europeans brought cats, *Felis catus*, and foxes, *Vulpes vulpes*, in the past several hundred years – Strahan 1995; Low 1999). In contrast, Kawau Island is an exclusive predator-free resort, nature reserve, and farming island where some animals may be occasionally exposed to a housecat or to a domestic dog. Farm dogs may have harassed the tammars around Rotorua, but the wallaby population has grown virtually un-checked by predation and was, just before our observations, reduced by air-dropping poisoned carrots and shooting.

Modifying time allocation as a function of group size is only beneficial when animals are aggregated. Tammars spend their days mostly alone in dense cover but emerge and aggregate in open grasslands to forage in large aggregations of several to > 20 animals after sunset (Kinloch 1973; Inns 1980; Blumstein & Daniel 2002). Aggregation and group size effects are likely an effective antipredator behavior against mammalian predators. Both extant eutherian and presumably extinct marsupial predators may hunt at night (nocturnality is ancestral in marsupials – Coulson 1996). In contrast, group size effects should be largely ineffective against predation by diurnal raptors because wallabies spend their days alone in dense cover where there is limited risk of raptor predation. Carpet pythons hunt tammars by waiting for an individual to cross their path (B.J. Wykes, pers. comm.), suggesting that tammars might not benefit from either dilution or detection effects to minimize the risk of snake predation; being killed by a cryptic sit and wait predator is akin to stepping on a mine – more eyes and ears may not reduce the risk of predation.

There has been a recent call for more attention to be paid to the combined effects of multiple predators on prey (Sih et al. 1998; Magurran 1999; Krams 2000). The multi-predator hypothesis predicts that the presence of a single predator may be sufficient to explain evolutionary persistence of antipredator behavior – even that for formerly present predators (D.T. Blumstein, unpublished data). However, it is unknown whether or not group size effects and predator recognition abilities can be maintained following a period of complete isolation and the New Zealand tammars, thus, offer a unique opportunity to ask this question.

Using similar methodologies for previous studies of group size effects (Blumstein & Daniel 2002) and for previous studies of predator recognition in Kangaroo Island tammars (Blumstein et al. 2000), we asked the following three questions. (i) Do New Zealand tammars have group size effects? (ii) Can they respond fearfully to the visual stimuli? (iii) Can they respond to the sounds of predators? To ask these questions, we made one key, but reasonable, assumption: 130 yr ago, before the introduction to New Zealand, animals from mainland South Australia had group size effects and that they had similar, or more refined, predator recognition abilities than Kangaroo Island animals which were isolated from mammalian predators for 9500 yr.

Methods

Group Size Effects

Subjects and study sites

We studied group size effects in tammar wallabies in four locations where they existed with either: (i) avian and reptilian predators (Garden Island, Australia – 32°09′S, 115°40′E); (ii) mammalian, avian and reptilian predators (Tutanning Nature Reserve, Australia – 32°32′S, 117°19′E); (iii) avian predators only (Kangaroo Island, Australia – 35°52′S, 136°53′E), or (iv) no predators (Rotorua, New Zealand – 38°20′S, 176°25′E). Details about the study sites can be found elsewhere (Blumstein 2002).

Data collection

We video-recorded for 5 min the focal animal samples from sunset to 7.6 h after sunset (Garden Island, sunset to 4.5 h after; Tutanning, 0.3 h after to 4.3 h after sunset; Kangaroo Island, sunset to 4.8 h after; Rotorua, 1.8 to 7.6 h post-sunset) on days without heavy rain. We stood or sat in locations where we did not obviously influence our focal subject's behavior.

We observed individuals as they moved out of cover to forage. We affixed image intensifiers (ITT Nightcam 300, ITT Industries, White Plains, New York, USA) with 80–200 mm zoom camera lenses (Nikkor, Nikon Corporation, Tokyo, Japan and Minolta, Konica Minolta Holdings, Inc., Tokyo, Japan) to the video cameras (Panasonic VX77A, Matsushita Electric Corporation, Osaka, Japan). We illuminated the image-intensified video field with either unfiltered, red-filtered, or yellow-filtered 1 W headlamps (Petzl, Crolles, France). We observed no difference in the behavior of animals illuminated with the different color lights, nor did we detect any obvious effect of this low-level illumination (see also Blumstein et al. 1999).

Individuals were neither captured, nor marked. To avoid observing individuals more than once, we walked systematically through the meadows in which animals foraged and did not double-back on our paths. Ultimately, there were more animals at each site than subjects and we are confident that most of the observations come from different individuals.

Group size is one of the most important variables in explaining variation in wallaby time allocation (Blumstein et al. 2002). At the beginning of each focal sample we noted the number of conspecifics within 10 m of the focal subject; a definition of group size previously demonstrated to be salient to tammars (Blumstein & Daniel 2002). Solitary animals were scored as being in a group size of one.

We scored videotaped focals using event-recording software and noted the onset of each bout of: foraging (on the ground and on shrubby vegetation above the ground); looking while crouching, standing, or while rearing up (a look was scored each time an individual moved its head and fixated); locomotion – defined as pentapedal walking (wallabies move their back legs forward while balancing on their forepaws and tail) and hopping; grooming; affiliative behavior (sniffing); and aggressive behavior (displacements). We also noted when animals went out of sight and when they were back in sight. We calculated the proportion of time allocated to each behavior as a function of the total time an animal was in sight; our analyses are restricted on the time allocated to the two most common behaviors – foraging and looking.

Statistical analyses

We excluded focal samples where animals were in sight for < 2 min, and focals where animals, while in sight, were obstructed by vegetation or terrain in a way to prevent reliable scoring. We aggregated our set of focal observations to obtain the best possible estimate of the group-size effect. For each individual observed at each group size (defined as the number of conspecifics within 10 m), we first calculated the percentage of time allocated to foraging and vigilance (as a function of time in sight) and then averaged the individual values to obtain a single score for each group size. Antipredator models of vigilance and foraging group size effects predict a logarithmic relationship between group size and time allocation, but linear group size effects could still be expected (Blumstein et al. 2001a). We therefore regressed our aggregated group size against time allocation and fitted two models to these data – a logarithmic model and a linear model. We calculated the adjusted R^2 for each of these models and illustrate group size effects, when significant, with the model that explained more variation. To formally compare the R^2 of different models, we would need to have had a greater range of group sizes. We report both linear and logarithmic adjusted R^2 values and note that the model that explained more variation, typically explained substantially more variation. We then restricted the range of group sizes used to fit the regression models to $N = 1$ to 5 to compare models fitted with the same range of data.

Strictly, our sample size is four populations. We use regression analyses to define the presence or absence of group size effects (the trait of interest) as a function of the presence or absence of some or all predators in each population. While not entirely correct (because observations across sites were not simultaneously collected in a randomized fashion), we also fitted linear models that included our measures of time allocation as the dependent variables, with log group size, location, and the interaction between group size and location as independent variables. A significant interaction would suggest that group size effects varied by population.

Predator Recognition

Subjects and husbandry

Fifteen tammar wallabies (10 males, five females – two had pouch young) were wild-caught by a professional trapper on Kawau Island, New Zealand (36°25′S, 174°53′E) and were transported to Massey University for testing. When not being tested, the animals were housed socially in groups of five, under cover with ambient light, in a large 'wool-shed' where they were provided ad libidum water and food (rabbit pellets and carrots). All animals appeared remarkably calm, and the experiments began after 9 d of habituation to captivity. For testing, subjects were moved to one of four 2.8 × 5.2 m testing arenas constructed within a large covered building with a 12 h light:dark schedule. In addition to background lights, two 75 W light bulbs illuminated each arena. Each arena had one stage, onto which a test or control stimulus would suddenly appear on a cart from behind a curtain. Subjects were given 4 d to habituate to this new environment during which time they were trained to feed on a large handful of grated carrots at a location 1.5 m away from the stage. In addition to carrots, animals had access to ad libidum water and were fed half of their daily ration of rabbit pellets twice each day.

Stimulus presentation and analysis

Detailed presentation methods generally followed those reported in Blumstein et al. (2000). Briefly, on successive mornings (within 3 h of 'sunrise'), tammars were baited to the central location and exposed (in a random order) to models or to taxidermic mounts of predators (a mounted cat, a mounted fox, or foam model thylacine – see Blumstein et al. 2000 for images of all stimuli), or control stimuli (a mounted tammar, the cart by itself without any additional stimulus, or a blank 'treatment' in which nothing was presented). On successive afternoons (within 3 h of 'sunset'), tammars were baited to the central location and were then exposed (in a random order) to the sounds of predators (dingoes, wedge-tailed eagles), predator-related sounds (foot-thumps), or control stimuli (the call of an Australian magpie – *Gymnorhina tibicen*, or a blank 'treatment' – spectrograms of stimuli in Blumstein et al. 2000). Stimuli were played back using either a cassette player or a PowerBook 100 computer, through a Sony SRS-77G powered speaker, at an average of 93.5 dB measured 1.0 m from the speaker (thumps = 86.2 dB; dingoes = 95.6 dB; eagle = 98.0 dB; magpie = 94.2 dB). An error presenting acoustic stimuli resulted in two subjects being given each other's stimuli on one of the experimental days. We therefore removed both individuals from subsequent analyses of acoustic data.

Subjects were videorecorded for 1 min before stimulus presentation, 1 min during stimulus presentation. One observer scored the videotapes using an event recorder. We calculated the percentage time allocated to three common behaviors – foraging, heightened vigilance, and locomotion (see Blumstein et al. 1999 for an ethogram, and Blumstein et al. 2000 for a justification of these behaviors to study predator recognition).

Statistical analyses

For the visual stimuli, we ignored the first 15 s of stimulus presentation because all animals oriented to the stimulus presentation. We focused instead on the response during the remaining 45 s of stimulus presentation and calculated the time allocation for each of those three 15 s time intervals. Each of these time intervals was compared with a 1 min baseline period prior to stimulus presentation and differences in these responses were compared with a two-factor repeated-measures ANOVA. Time since stimulus presentation significantly influenced responsiveness, however we focused on the main effect of stimulus type and on the interaction between type and time to understand wallaby predator recognition. For these repeated-measures ANOVAs we report Huynh-Feldt corrected p-values unadjusted for multiple comparisons (Carmer & Swanson 1973). Residuals from these linear models were examined and appeared to be normally distributed. In addition, we noted whether or not each subject foot-thumped at any time during the 1 min visual stimulus presentation, and analyzed the results using a Cochran's Q test followed up by post-hoc pair-wise McNemear's tests. For the acoustic stimuli, the time allocation for the three behaviors was calculated for the 15 s time interval that contained the acoustic stimulus (or blank control), and compared with a 1 min baseline period prior to stimulus presentation. The difference in time allocation from baseline as a function of stimulus type was compared using a one-way repeated-measures ANOVA. Residuals from these linear models were examined and appeared to be normally distributed. Wallabies never thumped during, or following, playback.

Results

Group Size Effects

We conducted 136 focal animal samples on Garden Island (25 adult females, 12 adult males, 80 unsexed adults, six sub-adults and 13 individuals that we could neither accurately sex nor accurately discriminate between adult and subadult age classes), 104 at Tutanning (15 adult females, 13 adult males, 49 unsexed adults, seven unsexed subadults and 20 that we could neither accurately sex nor accurately discriminate between adult and subadult age classes), 141 on Kangaroo Island (22 adult females, two subadult females, 15 adult males and one subadult male, 92 unsexed adults and nine unsexed subadults), and (because we studied the tammars soon after an effective poisoning campaign) 61 in New Zealand (five adult females, six adult males, 29 unsexed adults, two unsexed subadults, and 19 that we could neither accurately sex nor accurately discriminate between adult and subadult age classes). The number of wallabies within 10 m ranged from one to 11, but at times there were > 20 within 50 m on the densely packed Garden and Kangaroo islands.

Tammars from the three populations with predators – Garden Island, Tutanning, and Kangaroo Island – had significant group size effects for both foraging and looking, while the predator-free New Zealand population did not (Fig. 1). Logarithmic models explained more variation than linear models in the time allocated to looking as a function of group size for all populations where there was a relationship (Garden Island log adj. $R^2 = 0.59$; linear adj. $R^2 = 0.44$; Tutanning log adj. $R^2 = 0.58$; linear adj. $R^2 = 0.42$ Kangaroo Island log adj.

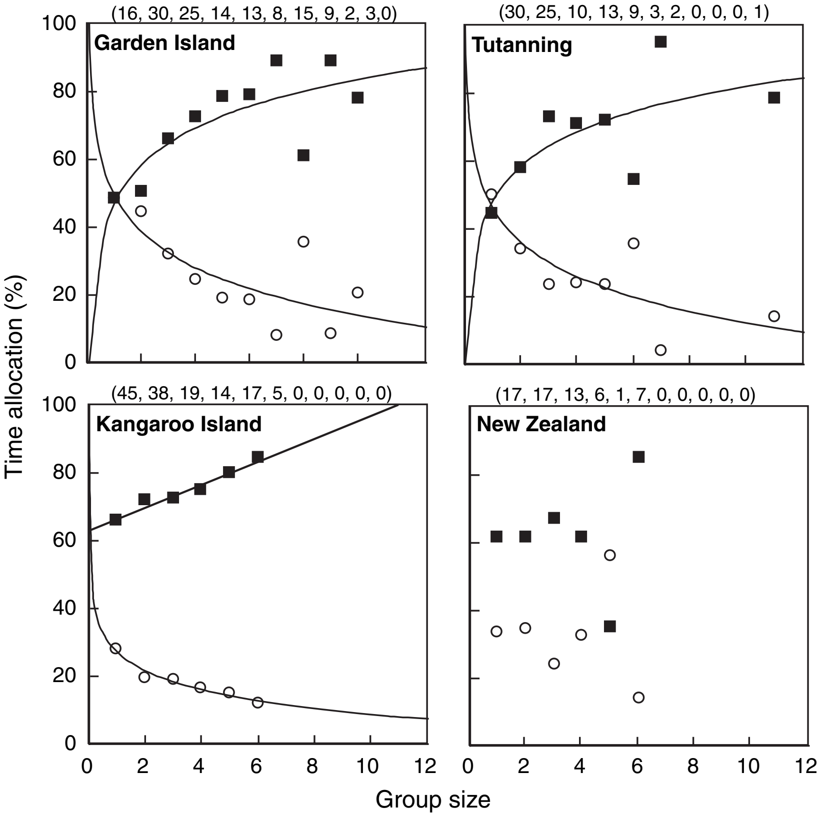

Fig. 1: Average time allocated to looking (open circles) and foraging (filled squares) as a function of group size (total N conspecifics within 10 m of a focal individual – including that focal individual) for tammar wallabies in four different locations. Linear and logarithmic regression models were fitted to the data; the better fitting significant model is illustrated. Note: this figure fits regressions to the data set that included all observed group sizes. Sample sizes for each group size are listed above each graph

$R^2 = 0.93$; linear adj. $R^2 = 0.83$). Logarithmic models explained more variation than linear models for the time allocated to foraging on Garden Island (log adj. $R^2 = 0.59$; linear adj. $R^2 = 0.45$) and Tutanning (log adj. $R^2 = 0.42$; linear adj. $R^2 = 0.27$), but not on Kangaroo Island (linear adj. $R^2 = 0.93$; log adj. $R^2 = 0.89$).

When we restricted the regression analysis to include only those estimates of time allocation from N = 1 to 5 for each site, we again found significant group size relationships at Garden Island (foraging: linear adj. $R^2 = 0.94$, $p = 0.004$; vigilance: linear adj. $R^2 = 0.97$, $p = 0.002$), Tutanning (foraging: log adj. $R^2 = 0.87$, $p = 0.013$; vigilance: log adj. $R^2 = 0.88$, $p = 0.013$) and at Kangaroo Island (foraging: log adj $R^2 = 0.91$, $p = 0.008$; vigilance: adj. $R^2 = 0.91$, $p = 0.008$), but not at New Zealand (foraging: adjusted $R^2 < 0.01$, $p = 0.39$, adjusted $R^2 = 0$, $p = 0.609$ with N = 5 excluded because of its single observation; vigilance:

adjusted $R^2 < 0.01$, $p = 0.491$ with $N = 5$, adjusted $R^2 < 0.01$, $p = 0.579$ with $N = 5$ excluded).

We found a moderately significant interaction between log group size and location for the time wallabies allocated to foraging ($p = 0.052$), and the time wallabies allocated to vigilance ($p = 0.058$). In both models, population, and log group size were highly significant main effects ($p < 0.001$).

Predator Recognition

There were no significant interactions between stimulus type and time (foraging $p = 0.203$; heightened vigilance $p = 0.071$; locomotion $p = 0.278$). We thus focus on the main effects of stimulus type. Wallabies responded to visual stimulus presentations (Fig. 2) by suppressing their foraging (tammar wallaby, $p = 0.046$) and increasing their locomotion ($p = 0.0002$); heightened vigilance was not significantly modified ($p = 0.155$). Comparisons of the foraging response revealed that only the fox and the thylacine significantly suppressed foraging compared with the blank (fox $p = 0.024$; thylacine $p = 0.003$), only the thylacine suppressed foraging compared with the cart ($p = 0.048$), and there was a non-significant tendency for the thylacine to suppress foraging compared with the wallaby ($p = 0.079$). There was also a tendency for the thylacine to suppress foraging compared with the cat ($p = 0.055$). Comparisons of the locomotion response revealed that all stimuli elicited more locomotion than the blank, which elicited no change in locomotion (blank = −0.02% ± 0.012 SE; all p-values <0.036). Only the thylacine elicited significantly more locomotion than the cart ($p = 0.038$). There were non-significant tendencies in both the fox versus cart comparison ($p = 0.088$), and the thylacine vs. wallaby comparison ($p = 0.094$). Both the fox ($p = 0.029$) and the thylacine ($p = 0.011$) elicited significantly more locomotion than the cat.

There was no difference in the probability that individuals thumped to the different stimuli (blank = 0 thumps, cart = 4, wallaby = 2, cat = 3, fox = 4, thylacine = 6; Cochran's $Q = 8.8$, $p = 0.117$); nevertheless, McNemear's tests revealed significantly more thumps were elicited by the thylacine than the blank ($p = 0.031$).

After hearing any sound (Fig. 3), wallabies tended to increase their vigilance ($p = 0.074$), they decreased their foraging ($p = 0.004$), and they did not modify their time allocated to locomotion ($p = 0.74$). However, none of the individual stimuli differed significantly from each other. If present, significant differences were between the blank and the stimuli (all vigilance p-values <0.04; all foraging p-values <0.02; all locomotion p-values >0.32).

Discussion

These results are consistent with the key prediction of the multi-predator hypothesis (D.T. Blumstein, unpublished data): populations without any predators will lose antipredator behavior, but the presence of any predators is

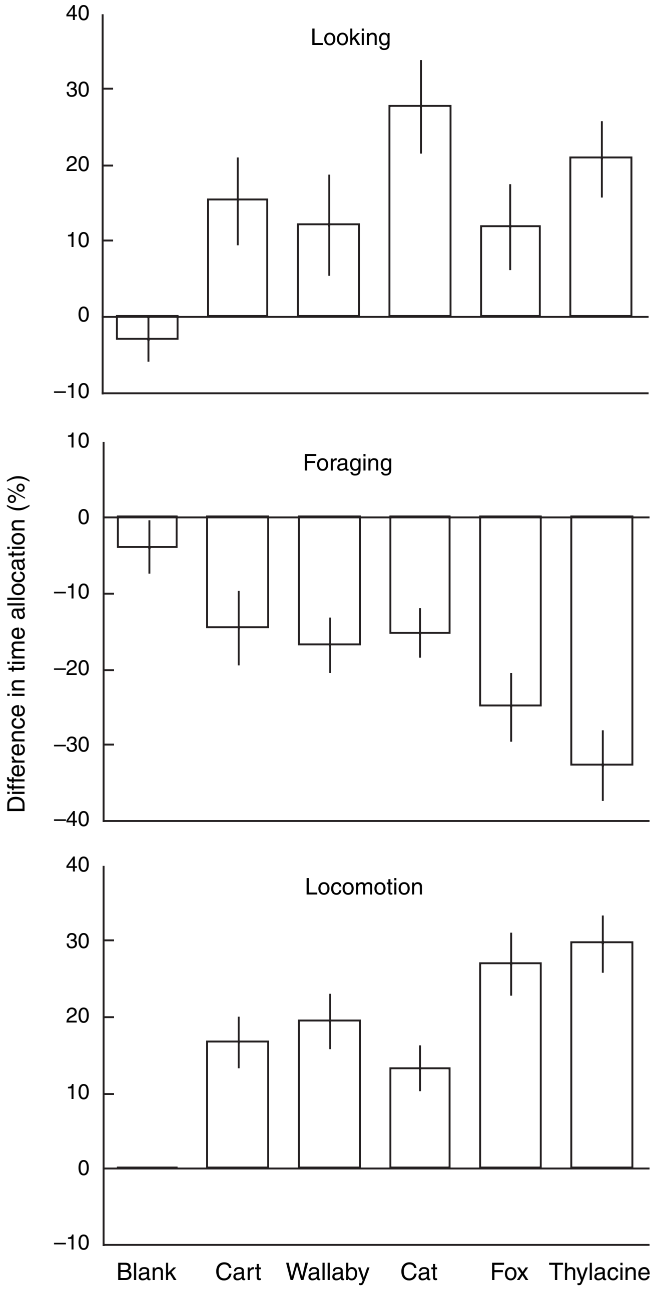

Fig. 2: Percentage difference ($\bar{x}$ ± SE) in time Kawau Island tammar wallabies allocated to looking, foraging, and locomotion in the final 45 s of a 60-s visual stimulus presentation compared with baseline

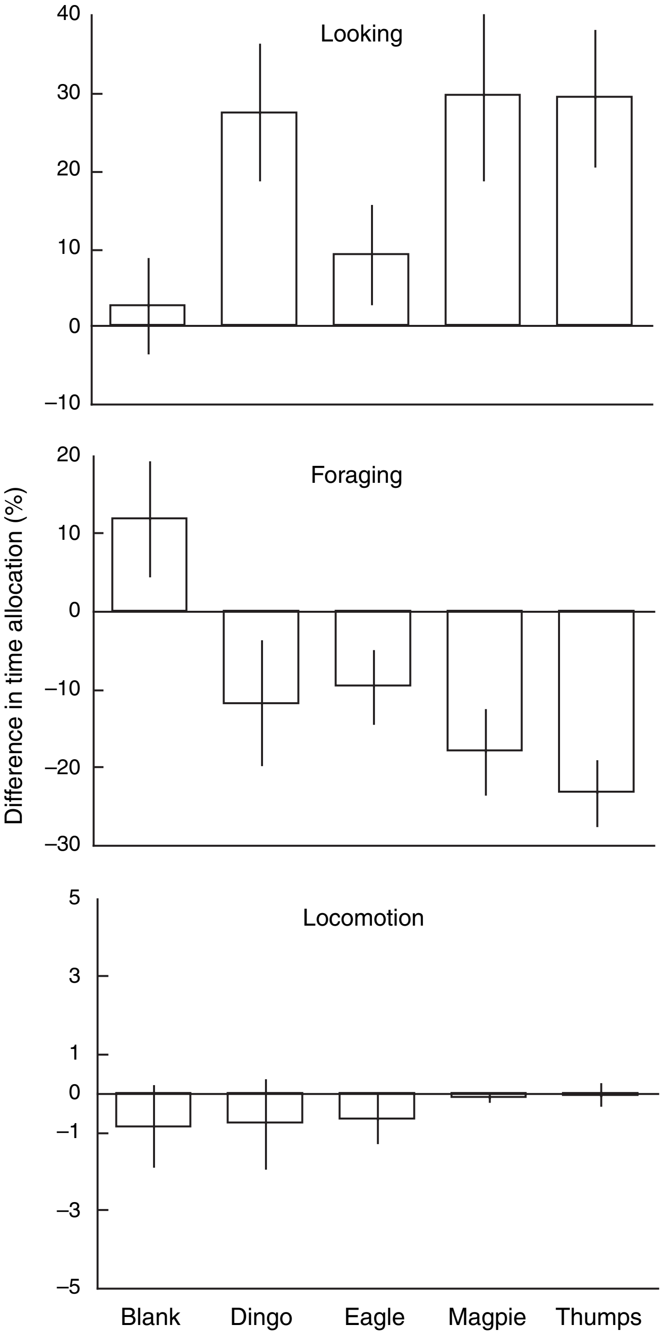

Fig. 3: Percentage difference (x̄ ± SE) in time Kawau Island tammar wallabies allocated to looking, foraging, and locomotion in the 15 s during and after acoustic stimulus presentation compared with the baseline. Note that scales differ to facilitate comparison with each dependent measure

sufficient to maintain antipredator behavior – even that which is effective for species not present. Specifically, tammar wallabies from locations with one or more predators retained group size effects, while tammars from a predator-free population did not. Additionally, tammars from a predator-free population did not discriminate among taxidermic mounts or models of mammalian predators, whereas tammars from Kangaroo Island – an island without mammalian predators but with aerial predators – retained the ability to recognize novel mammalian predators (Blumstein et al. 2000).

The loss of beneficial group size effects occurred quickly – in as few as 130 yr – which suggests some cost for their maintenance in the absence of all predators. At this point, we can only speculate that when released from predation risk, intraspecific competition may emerge. A study of quokkas (*Setonix brachyurus*), a small macropodid marsupial isolated from predators for 7000 yr, found that they retained linear group size effects (Blumstein et al. 2001b).

Unlike tammars from Kangaroo Island which were able to recognize and respond to novel mammalian predators (the fox and cat; Blumstein et al. 2000), tammars from Kawau Island responded selectively only to the model thylacine. One interpretation is that because individuals had variable responses, we had insufficient power to detect an effect. We think this is unlikely for the following reasons. First, we used similar sample sizes as those used in the previous study (15 subjects vs. 19 subjects used in Blumstein et al. 2000). Secondly, we employed powerful repeated-measures analyses to account for the variation in individual's responses. Most importantly, the pattern of responses in the two studies is qualitatively different: in this study the thylacine model elicited the largest response.

Another interpretation of this result is that Kawau tammars retained a specific ability to recognize thylacines or thylacine-like animals. This might result from the relative recency of experience with thylacines that lived on mainland Australia until 2000–3000 yr ago (Kohen 1995), and presumably more recent exposure to dingoes. In contrast, there is no evidence of thylacines (or dingoes) on Kangaroo Island since its isolation 9500 yr ago.

However, for the following reasons, we feel that these results are most likely to represent a less specific predator-recognition template that relies on size. First, the thylacine was the largest stimulus and apparent size may be an important fear-eliciting stimulus (e.g. Menzel 1962; Evans et al. 1993). Secondly, the sight of the thylacine decreased foraging and increased locomotion compared with the cat. This is notable both because the cat was a type of predator, and also it was the smallest animal stimulus. Thus, Kawau Island tammars did not appear to have a template that permitted them to recognize cats as predators. Moreover, the fact that they did not differentiate most controls from the other predatory stimuli suggests that while they attended to movement and the presentation of objects, they did not have the more specific visual predator recognition template found in Kangaroo Island animals.

Together our results suggest that Kawau Island tammars possess only a crude visual predator recognition template. We infer that the presence of wedge-tailed eagles on Kangaroo Island was sufficient to maintain a rather specific mammalian predator recognition template in Kangaroo Island tammars. This is remarkable because Kawau animals have been isolated from all predators for only 130 yr, while the Kangaroo Island animals had been isolated from mammalian, but not avian predators for 9500 yr.

While the multi-predator hypothesis would suggest that this recognition of terrestrial predators was maintained by natural selection to respond appropriately to aerial predators, on a proximate level, attacks by eagles may act as ‘priming agents’ – which affect both attentional and emotional components of antipredator behavior. For instance, snake-naïve squirrel monkeys (*Saimiri sciureus*) raised with live and moving food, respond fearfully to snakes while snake-naïve monkeys raised without live food failed to respond fearfully to snakes (Masataka 1993). Thus, it is possible that experience with a presently unspecified priming stimulus (or stimuli) may underlie the persistence of mammalian predator recognition in Kangaroo Island tammars. If so, the priming stimulus must be absent on Kawau Island. At this point we know that wedge-tailed eagles are absent on Kawau Island.

Tammars did not respond to the sounds of predators. The fact that they failed to respond to the played back foot thumps is consistent with the previous interpretation (Blumstein et al. 2000) of an experienced-based mechanism for acoustic predator recognition. Wild-caught tammars on Kawau probably rarely heard other individuals foot-thumping where they live in relatively low densities (B.P. Springett, pers. obs.). In contrast, the Kangaroo Island animals were housed socially and densely at the Macquarie University Fauna Park where they heard foot thumps on a daily basis.

The mechanism(s) responsible for predator recognition have important implications for conservation. For tammars, visual predator recognition templates can lose specificity quickly. A parallel set of experiments with Kangaroo Island animals has demonstrated that fox-elicited antipredator behavior can be enhanced following training, and that training specifically enhances predator recognition (Griffin et al. 2001). Kawau Island animals will be translocated to recover the mainland South Australian population. Most such translocations fail because predators kill vulnerable prey (Beck et al. 1991; Short et al. 1992; Miller et al. 1994). Our results suggest that predator training may be a useful strategy to increase translocation success if innate, but relatively unspecific, mammalian predator templates can be focused.

In conclusion, the multi-predator hypothesis (D.T. Blumstein, unpublished data) has both explanatory and predictive power. Assuming similar costs for their expression in the absence of predators, species with some predators are predicted to retain antipredator behavior evolved to deal with formerly important predators, while those without any predators may lose it. The rate of loss may reflect underlying maintenance costs (van Damme & Castilla 1996). Given the rapid evolutionary loss of tammar wallaby antipredator behavior, we can assume that modifying time allocation as a function of group size and predator recognition must be costly in the absence of all predators.

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