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How does the presence of predators influence the persistence of antipredator behavior?

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Abstract

We developed a virtual world to study the effect of predators on predator recognition. We trained a neural network to discriminate between the shapes of simulated aerial and terrestrial predators and non-predators. Then, the network's weighting values were fixed into the genomes of a set of autonomous agents. These animats were required to eat, avoid death due to starvation, and avoid predation, by fleeing from approaching predators. We systematically varied the predator's lethality, the mutation rate, the cost of fleeing a predator, and the presence or absence of aerial and terrestrial predators. We used ANOVA to analyse the average recognition ability (a measure of directional selection) and the standard deviation of recognition ability (a measure of relaxed selection) after 500 generations of selection. Mutation rate and the cost of flight had the greatest effect on both the average and standard deviation of recognition abilities. The loss of all predators relaxed selection on predator recognition abilities. The loss of specific predators had complex effects on recognition abilities. Persistence is largely influenced by escape costs.

Keywords: Animat model; Evolutionary persistence; Relaxed selection

1. Introduction

Species may lose their predators naturally (through range expansions or extinction), or un-naturally (when animals are brought into captivity). In response to a loss of predators, costly antipredator behavior is often lost (e.g. Diamond, 1990; Berger, 1998; Magurran, 1999; Berger et al., 2001). Indeed, species on isolated islands, such as the Galápagos, are often described as being predator-naïve (Darwin, 1839; Lack, 1947; Curio, 1966). The consequences of this loss may be profound if predator-naïve species re-encounter their predators (McLean et al., 1999; Griffin et al., 2000). Loss of antipredator behavior, however, is not inevitable and there are cases where antipredator behavior persists after the loss of predators (e.g. Byers, 1997; Coss, 1999; Blumstein et al., 2000; Blumstein and Daniel, 2002).

There are several inter-related hypotheses to explain the persistence of antipredator behavior under relaxed selection (i.e. the loss of one or more types of predators). The "ghost of predators past" hypothesis (Byers, 1997; Peckarsky and Penton, 1988) simply says that a species subject to past selection for antipredator behavior will retain it if it is not too costly (e.g. Neill, 1990). The "pleiotropic" (Byers, 1997; Coss, 1999) and "functional integration" (Coss, 1999) hypotheses emphasize that behaviors used when dealing with predators may have multiple functions or otherwise be genetically linked. Thus, antipredator behavior may be retained simply because there is selection on a locus maintained for other reasons. Most species have more than a single predator and rare predators may have a significant effect on antipredator behavior (Lima, 1992). There has been a recent call for more attention to be paid to the combined

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effects of multiple predators on prey (Lima, 1992; Sih et al., 1998; Magurran, 1999; Krams, 2000). The "multi-predator hypothesis" builds on previous hypotheses about persistence and predicts that the presence of a single predator may be sufficient to explain evolutionary persistence of antipredator behavior—even for formerly present predators (Blumstein et al., 2004). Pleiotropy and/or functional integration may provide the necessary selection to maintain complex traits and we generally expect complex traits to not assort independently because a minor change could have major negative consequences (Fisher, 1958). When antipredator behavior has pleiotropic effects, and/or when it does not assort independently, species living with multiple predators may have evolved specific traits to reduce predation risk in response to each predator, but their expression is not predicted to vary independently. Imagine a young ungulate that must be cryptic and immobile to avoid predation. An individual without both traits would be selectively disadvantaged. Similarly, being able to respond to one but not another type of extant predator would put individuals at a selective disadvantage. Thus, the presence of a single predator should maintain antipredator adaptations for predators no longer present.

The presence of predators, per se, may not be the only factor influencing persistence. Generally, we should expect costly behaviors to be lost, while low-cost behaviors may persist. Very costly traits, such as those that reduce reproductive success (e.g. those subject to sexual selection), seem to respond quickly to relaxed selection brought about by the removal of predators (Endler, 1980; Endler and Houde, 1995). Predator lethality affects antipredator behavior (Brown, 1999; Brown and Kotler, in press) and it should influence persistence.

We developed a virtual world (based loosely on the tammar wallabies (*Macropus eugenii*) studied by Blumstein et al., 2000; Blumstein and Daniel, 2002, 2004) to study the conditions under which predator recognition abilities would persist following the loss of some or all of a species' predators. We first developed a neural network that was trained to discriminate predators (raptors or mammalian predators) from non-predators (smaller birds or macropodids). The use of neural networks to study questions in animal behavior is growing (e.g. Bateson and Horn, 1994; Enquist and Arak, 1994; Hurd et al., 1995; Phelps et al., 2001; Ryan et al., 2001). Neural networks are characterized by a series of "neurons" that are connected to each other in varying degrees. The strength of a connection can be defined as a "weight". The process of "training the network" creates weights that optimize the discrimination. Once the network was able to discriminate between predators and non-predators, we fixed the weights in this network and created a "genome" of weights that was subject to mutation. This genome was placed into animats—autonomous agents—that had to avoid death from starvation and predation. Thus, the second phase of the simulation employed a genetic algorithm (Sumida et al., 1990) to study the conditions under which predator discrimination abilities persist. Agent-based modeling is becoming increasingly common in animal behavior research (e.g. Pepper and Smuts, 2002; Ruckstuhl and Kokko, 2002; Coss et al., 2005), and others have used genetic algorithms to help develop a neural network (e.g. Ezoe and Iwasa, 1997; Kamo et al., 1998; Yao, 1999; Phelps and Ryan, 2001). However, the combination of neural networks and genetic algorithms acting within an agent-based model is relatively recent (Lee, 2003). To study the main prediction of the multi-predator hypotheses (namely, that we should expect the presence of one predator to explain the persistence of antipredator behavior but the complete elimination of predators to abolish antipredator behavior) we manipulated the presence or absence of specific predators. Because other things influence the persistence of antipredator behavior, we also manipulated mutation rate, the cost of flight, and predator lethality. We quantified predator recognition abilities directly by presenting our animats with a virtual predator and recording the network's classification: a probability distribution over the four classes encountered (i.e. the shapes of simulated aerial and terrestrial predators and non-predators). We searched for evidence of directional and relaxed selection in response to the loss of one or all predators. Directional selection would be inferred if the average predator recognition abilities shifted, while relaxed selection would be inferred if the variation in predator recognition abilities increased (e.g. Endler, 1986; McPhee, 2003).

2. Methods

We created a simulation environment where animals foraged in a forest clearing and could retreat to safety in cover that surrounded it. Specifically, our virtual world consisted of simulated wallabies (with a diameter of 3 pixels each) foraging in a square meadow surrounded by protective cover (500 × 500 pixels total area) that contained other wallabies as well as a combination of predators and non-predators (also 3 pixels each). The detection distance of both predators and prey was identical; upon detection, predators approached wallabies and, if classified as a predator, wallabies fled. Wallabies could escape a predator by out-maneuvering it, reaching protective cover, or by having the predator terminate attack because another wallaby entered its detection range. When in cover, the wallabies were safe from predation and predators were unable to detect them. However, to avoid starvation, wallabies had to forage in the open. Food randomly replenished itself in the open, and wallabies had to encounter food to eat. In cover there were only other wallabies moving around, but in the open, there were both non-predatory and predatory agents.

Our predators were generalists that took two forms: birds and mammals; birds moved twice as fast as mammals. By varying the speed, we varied predator lethality: fast moving predators encountered and killed wallabies at higher frequencies than slow moving predators. There were predatory and non-predatory birds and mammals. Predatory mammals were larger and roughly resembled a canid, while predatory birds resembled a raptor (Fig. 1). Predators were always larger than non-predators. Overall, non-predatory birds were more similar to predatory birds (36% of the non-predator's body was identical to the predator's body) than were non-predatory mammals and predatory mammals (27% similarity). We fixed the maximum number of wallabies. Wallabies had to forage while avoiding predators (in our virtual world we assumed that predator recognition and response were integrated), but behavior was not state dependent; wallabies with low energy reserves were not more likely to leave cover to forage. While we acknowledge the importance of state-dependent behavior, we made this simplifying assumption to reduce the number of variables requiring analysis. Rather, they moved around randomly encountering food or starving if they did not. While not specifically quantified, we did observe wallabies starving while fleeing agents.

At the end of a generation, wallabies reproduced to replace those that died. Reproduction was asexual and those with greater energy reserves contributed proportionally more to replacing missing wallabies. Below we describe, in detail, the neural network and genetic algorithm used to study discrimination, along with the precise experiments conducted in this virtual world.

2.1. Using a neural network to discriminate among predators

For each wallaby, we created a two-layer neural network with probabilistic outputs. Such a network can be thought of as a machine that decides the probability, based on some input, that an exemplar falls into one of four classes: aerial predator, aerial non-predator, terrestrial predator, terrestrial non-predator. There are a variety of computational machines that could be used for classification (Duda et al., 2001). We chose a neural network with probabilistic outputs for three reasons.

First, animal brains are composed of webs of simple processing units with plastic, synaptic efficacies between them. Thus, there is an analogy between brains and artificial neural networks (Churchland and Sejnowski, 1992).

Aerial

```
     Non-predator                  Predator

0 0 0 0 0 0 0 0 0 0        0 0 0 0 X X 0 0 0 0
0 0 0 0 0 0 0 0 0 0        0 0 0 0 X X 0 0 0 0
0 0 0 0 X X 0 0 0 0        0 0 0 X X X X 0 0 0
0 0 0 X X X X 0 0 0        X X X X X X X X X X
0 0 X X X X X X 0 0        X X X X X X X X X X
0 0 0 0 X X 0 0 0 0        X X X X X X X X X X
0 0 0 0 X X 0 0 0 0        0 0 0 0 X X 0 0 0 0
0 0 0 0 0 0 0 0 0 0        0 0 0 0 X X 0 0 0 0
0 0 0 0 0 0 0 0 0 0        0 0 0 0 X X 0 0 0 0
0 0 0 0 0 0 0 0 0 0        0 0 0 0 0 0 0 0 0 0
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Terrestrial

```
     Non-predator                  Predator

0 0 0 0 0 0 0 0 0 0        0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0        0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0        0 0 X 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0        X X X X 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0        0 X X X 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0        0 0 X X X X X X 0 0
0 X X 0 0 0 0 0 0 0        0 0 X X X X X X X X
X X X X X X X 0 0 0        0 0 X X X X X X X 0
0 0 X X X X X 0 0 0        0 0 X 0 0 0 0 0 X 0
0 0 X 0 X 0 X X X X        0 0 X 0 0 0 0 0 X 0
```

Fig. 1. Prototypical exemplars of predatory and non-predatory agents. Aerial predators resembled a raptor, non-predators, a small bird. Terrestrial predators simulated a canid, non-predators, an herbivore. These prototypes were modified for the training phase. In the evolutionary phase, discrimination of the prototypes was tested at every generation.

Second, there is evidence that brains utilize some form of probabilistic assessment in making classifications and judgments based on peripheral sensory inputs. This evidence comes from both the cognitive sciences (Anderson, 1990; Gigerenzer and Murray, 1987; Gilovich et al., 2002; Kahneman et al., 1982; Oaksfordl and Chater, 2003) as well as other related fields such as artificial intelligence (Pearl, 1988).

Finally, the weights of a neural network (see below) are easily encoded as a genome, thereby enabling us to study the evolutionary persistence of classification following the removal of some or all types of predators.

Our network began with 100 input units representing the 10×10 matrix we used to draw agents (Fig. 1). Note: the visual display of the animats during simulation (i.e. 3 pixel diameter circles) is unrelated to the patterns representing their visual appearance used as input to the neural networks (see above). Each input unit was connected in a forward fashion (Hertz et al., 1991) to each of seven hidden units. We chose seven units empirically, based on the time it took to train the classifier with various numbers of hidden units. Each of the seven hidden units was associated with a 10×10 weight matrix w indicating the synaptic strength between it and the 100 inputs. The weight matrix provided a set of parameters by which a suitable algorithm could allow the network to "learn" the correct classification of each predator's or non-predator's pattern.

Given input pattern μ, and input vector ξ, hidden unit j produced output

$$V_j^\mu = g(h_j^\mu) = g\left(\sum_k w_{jk}\xi_k^\mu\right), \tag{1}$$

where the function g is the hyperbolic tangent function tan h. The nonlinearity provided by g is required in order to guarantee a differentiable surface for the learning algorithm.

The outputs of all seven hidden units represented a hidden output vector. Each hidden unit was connected, in a forward fashion, to each of the four output units (each representing one of the four types of agents). Each of these output units was associated with a 7 × 7 weight matrix indicating the synaptic strength between it and the 7 hidden units. For input pattern μ, output unit i produces for the final output

$$O_i^\mu = g\left(\sum_j W_{ij}V_j^\mu\right). \tag{2}$$

In this case the function g is the softmax function given by

$$\frac{\exp(O_i)}{\sum_j \exp(O_j)}, \tag{3}$$

where j ranges over all network outputs. The softmax function requires all network outputs to sum to unity so that they can be interpreted as probabilities of class membership (Hertz et al., 1991; Duda et al., 2001).

Each network was trained to correctly classify 100 test cases of each agent type. These test cases were created by randomly adding noise to the 10×10 prototypical exemplars of each agent type. For training we employed an augmented version of the BFGS algorithm (Broyden, 1970; Fletcher, 1970; Goldfarb, 1970; Shanno, 1970), which employs a minimum posterior, cross-entropy error function to find weight matrices that maximized the accuracy of the classifications. If the actual and target outputs of the network represent two probability distributions, then information theory suggests that their cross-entropy is a natural measure of their difference (Hertz et al., 1991). Thus, an entropy-based error function can be viewed as a natural system that learns the correct probabilities of a set of hypotheses represented by the output units (Hertz et al., 1991; Duda et al., 2001). It is this error surface that the BFGS algorithm minimizes, and the final trained network outputs compute the posterior probability of class ω given the input vector ξ

$$p(\omega|\xi). \tag{4}$$

We used the ANN:DTU Matlab Toolbox (MacKay, 1992a, b; Larsen and Hansen, 2002; http://mole.imm.dtu.dk/toolbox/ann/) to develop our neural network. We trained the network to an error threshold of 0.01. Thus, we considered a network that made 1% deviation from absolute certainty in classification as sufficiently discriminative. Network discrimination depends upon the number and type of the training patterns. The original batch of 800 training/validation patterns consisted of the original prototypes to which we added a random amount of noise (up to 10%). The training and validation patterns where then randomly chosen from this pool of 800. The noise prevented over-fitting and facilitated the generalization capabilities of the networks (Hertz et al., 1991; Duda et al., 2001). We fixed the number of training and validation patters to 200 each; 100 of these were predator variants, and 100 of these were non-predator variants. Each of these batches was then further divided so that half were terrestrial and half aerial.

2.2. *Using a genetic algorithm to study relaxed selection*

Once trained, the classification ability of each network was defined by its two weighting matrices. We directly encoded these matrices to produce a genome for each network phenotype (Mitchell, 1996). To do so, we encoded each matrix row-by-row as a vector and then concatenated the vector representing W onto the vector representing ω. We used this simulated genome to study the evolutionary persistence of predator recognition under different selective regimes.

Each "generation" had a fixed duration during which time the wallabies would have to avoid predators, and starvation. The genotype could mutate, at a variable rate, and the cost of locomotion could be varied. At the end of a generation, surviving wallabies reproduced asexually; fitness was proportional to its energy reserves and was specified as

$$\mathit{offspring}_i = \lfloor n * \mathit{fit}_i \rfloor, \tag{5}$$

where n was the total number of desired wallabies in each generation. The genomes of newly created wallabies were subjected to random point mutation reflecting the desired rate of mutation.

2.3. *Identifying the parameter space to study persistence*

With too much mutation, all discrimination was eliminated. We were unable to generate a sufficiently large selective pressure (by varying the relative cost of flight) to "recover" discrimination. Moreover, if the risky predator moved too quickly, all wallabies were killed before the end of a generation and the simulation ended. All wallabies were also killed if the generation was too long. If the cost of fleeing was too great, all wallabies starved. Thus, we systematically varied mutation rate, generation length, the cost of flight, and the speed of the predators until some wallabies always survived a 500-generation simulation cycle. This state space allowed us to examine the effect size of the different variables; parameters were not estimated from empirical data.

2.4. *Simulating relaxed selection*

Our basic runs had 30 wallabies and a total of 14 predatory and non-predatory agents to simulate a situation where there was strong selection for appropriate recognition. We varied the presence or absence of aerial and terrestrial predators, whether the predators moved at a different speed or not (in the fast case, aerial predators moved twice as fast as terrestrial predators and thus had increased "lethality"), mutation rate (0.001 or 0.0001 mutations/generation—these represent very high mutation rates—Baker et al., 1996, 1997), and the cost of fleeing a predator (1.5 or 15 energy units). The basic cost of "living" was 0.1 energy unit per time period. To simulate different selection regimes we created four types of simulation runs: the first run had an aerial and terrestrial predator, the second had neither an aerial nor a terrestrial predator, and the remaining two had one aerial or one terrestrial predator, respectively. When we eliminated a predator, we substituted it with a non-predator of the same hunting style. At the start of each generation, we "probed" the genome with the original prototypical exemplars and recorded the classification accuracy. Our simulation lasted 500 generations; each generation lasted 50 time steps. Each combination of parameters was replicated 10 times creating a set of 160 simulations. For each run, we calculated the average and standard deviation of the ability to differentiate aerial and terrestrial predators across the 500 generations.

We fitted the following ANOVA models to the mean and standard deviation of the classification scores. First, we used ANOVA to study the effects of the presence or absence of all predators on aerial and terrestrial predator recognition. We also included the fixed factors of mutation rate and the cost of flight. For this and other models, we interpret p-values<0.05 as significant and we focus on the partial-eta square as a measure of a variable's (or interaction's) effect size (Cohen, 1988). We elected to focus on the effect size of each parameter because this focuses on the relative importance of each variable (or interaction) and should be less sensitive to the absolute parameter values used. We then fitted a model that had mutation rate and cost of flight as fixed factors along with the presence or absence of aerial predators and the presence or absence of terrestrial predators.

3. Results

Tables 1 and 2 present our main results. They illustrate the effect sizes (presented as partial-eta squares) from the factorial ANOVA studying the effect of mutation rate, cost of escape (simulated by varying the energetic cost of escape relative to the basal metabolic rate), the presence of any predator (i.e. either or both aerial or terrestrial predators were present), and the relative difference in lethality (simulated by predator speed) on the persistence of predator recognition abilities. Within a table, larger effect sizes indicate a relatively more important variable (or interaction) in explaining the persistence of the ability to recognize terrestrial or aerial predators.

Mutation rate, cost of escape, predator lethality—directly, and acting through interactions—explained most of the variation in the average and the standard deviation of predator recognition abilities (Tables 1, 2). Predator recognition decreased and the variation in recognition increased with increasing mutation rate, cost of escape, and differential predator lethality. The partial eta-squares of the mutation rate had the single largest effect on recognition abilities. Consistently more variation was explained in the standard deviation of predator recognition abilities than the average recognition abilities. This is consistent with the hypothesis that selection on recognition abilities has been relaxed, rather than directionally changed.

The loss of all predators led to relaxed selection on predator recognition abilities two ways: directly, through the loss of predators, and indirectly through the interaction between mutation rate and the absence of predators (Table 1). There was no significant effect of the loss of all predators on average predator recognition abilities.

The loss of specific predators did not act directly on predator recognition abilities nor were the effects symmetrical. For instance, predator lethality had a directional and relaxed effect on aerial predator recognition abilities, but not terrestrial predator recognition abilities (Table 2). Additionally, variation in the average and standard deviation in terrestrial predator recognition was explained by interactions of mutation rate and lethality with the presence of terrestrial predators. The reciprocal was not true: the presence of aerial predators did not influence aerial predator recognition, nor did it influence terrestrial predator recognition.

4. Discussion

The multi-predator hypothesis predicts that the presence of other predators is an important determinant of whether or not antipredator ability persists following

Table 1
Effect sizes (partial-eta squares) for significant main effects and interactions calculated from a factorial ANOVA studying the presence of any predator on the standard deviation and average predator recognition abilities for terrestrial and aerial predators

	Terrestrial	Aerial
Standard deviation of recognition abilities		
Mutation rate	0.202	0.274
Cost of escape	0.019	0.043
Presence of any predator	0.014	0.016
Differential predator lethality		0.031
Mutation rate*Cost of escape	0.019	0.041
Mutation rate*Presence of any predator	0.013	0.012
Cost of escape*Presence of any predator		
Mutation rate*Cost of escape*Presence of any predator		
Mutation rate*Differential predator lethality		0.026
Cost of escape*Differential predator lethality	0.043	
Mutation rate*Cost of escape*Differential predator lethality	0.04	
Presence of any predator*Differential predator lethality		
Mutation rate*Presence of any predator*Differential predator lethality		
Cost of escape*Presence of any predator*Differential predator lethality		
Mutation rate*Cost of escape*Presence of any predator*Differential predator lethality		
Average recognition abilities		
Mutation rate	0.172	0.221
Cost of escape	0.016	0.037
Presence of any predator		
Differential predator lethality		0.035
Mutation rate*Cost of escape	0.016	0.032
Mutation rate*Presence of any predator		
Cost of escape*Presence of any predator		
Mutation rate*Cost of escape*Presence of any predator		
Mutation rate*Differential predator lethality		0.03
Cost of escape*Differential predator lethality	0.038	
Mutation rate*Cost of escape*Differential predator lethality	0.034	
Presence of any predator*Differential predator lethality		
Mutation rate*Presence of any predator*Differential predator lethality		
Cost of escape*Presence of any predator*Differential predator lethality		
Mutation rate*Cost of escape*Presence of any predator*Differential predator lethality		

Standard deviation of recognition abilities is a metric of relaxed selection and average recognition abilities is a measure of directional selection. More variation in recognition abilities was explained by relaxed selection ($R^2_{\text{terrestrial}} = 0.316$; $R^2_{\text{aerial}} = 0.408$), than by directional selection ($R^2_{\text{terrestrial}} = 0.281$; $R^2_{\text{aerial}} = 0.351$) suggesting that changes in these parameters act primarily by relaxing selection for recognition abilities.

the loss of a single predator. It makes no prediction about the relative effect size of having another predator around. We included other conceivably important variables in our simulation environment so as to evaluate the relative effect sizes of the presence of another predator on the persistence of predator recognition abilities.

Mutation rate had the greatest effect on predator recognition abilities. This was not entirely unexpected because high mutation rates would quickly eliminate functional traits. Moreover, because mutations are random we should expect the effect of mutations to increase the variation in response, and thus relax selection. If selection were held constant, mutation rates alone would increase variation. If mutation rates varied between populations (Baker et al., 1997; Møller and Mousseau, 2003), or if populations had different amounts of genetic variation to begin with (e.g. as might be found in a captive situation), lack of genetic variation could limit the rate of loss.

The cost of escaping predators was the second most important factor in explaining variation in recognition abilities. This is in agreement with the common finding that costly traits respond rapidly to a loss of predators. Interestingly, variation in recognition was primarily accounted for by the cost, rather than by interactions with the presence of predators. In our virtual world, wallabies lost energy if they incorrectly classified a common non-predator as a predator and avoided them. The risk of starvation alone, or the fitness cost of reduced fecundity could be sufficient to select against discrimination. Additional variation was explained by interactions of cost of escape with other variables. The cost of escape also interacted with predator lethality, as would be expected because lethal predator should select for animals willing to pay a greater cost to

Table 2
Effect sizes (partial-eta squares) for significant main effects and interactions calculated from a factorial ANOVA studying the presence of specific predator on the standard deviation and average predator recognition abilities for terrestrial and aerial predators

	Presence of aerial predator		Presence of terrestrial predator	
	Aerial	Terrestrial	Aerial	Terrestrial
Standard deviation of recognition abilities				
Mutation rate	0.286	0.203	0.211	0.287
Cost of escape	0.042	0.022	0.023	0.042
Differential predator lethality	0.050			0.050
Specific predator present				
Mutation rate*Cost of escape	0.037	0.022	0.023	0.037
Mutation rate*Differential predator lethality	0.050			0.050
Cost of escape*Differential predator lethality		0.046	0.048	
Mutation rate*Cost of escape*Differential predator lethality		0.043	0.045	
Mutation rate*Specific predator present				
Cost of escape*Specific predator present				
Mutation rate*Cost of escape*Specific predator present				
Differential predator lethality*Specific predator present			0.018	
Mutation rate*Differential predator lethality*Specific predator present			0.017	
Cost of escape*Differential predator lethality*Specific predator present				
Mutation rate*Cost of escape*Differential predator lethality*Specific predator present				
Average recognition abilities				
Mutation rate	0.237	0.181	0.188	0.236
Cost of escape	0.038	0.018	0.019	0.037
Differential predator lethality	0.049			0.049
Specific predator present				
Mutation rate*Cost of escape	0.031	0.018	0.018	0.031
Mutation rate*Differential predator lethality	0.048			0.047
Cost of escape*Differential predator lethality		0.041	0.043	
Mutation rate*Cost of escape*Differential predator lethality		0.038	0.039	
Mutation rate*Specific predator present				
Cost of escape*Specific predator present				
Mutation rate*Cost of escape*Specific predator present				
Differential predator lethality*Specific predator present			0.020	
Mutation rate*Differential predator lethality*Specific predator present			0.018	
Cost of escape*Differential predator lethality*Specific predator present				
Mutation rate*Cost of escape*Differential predator lethality*Specific predator present				

Standard deviation of recognition abilities is a metric of relaxed selection and average recognition abilities is a measure of directional selection. More variation in recognition abilities was explained by relaxed selection ($R^2_{\text{terrestrial, aerial present}} = 0.292$; $R^2_{\text{terrestrial, terrestrial present}} = 0.324$; $R^2_{\text{aerial, terrestrial present}} = 0.389$; $R^2_{\text{aerial, aerial present}} = 0.387$), than by directional selection ($R^2_{\text{terrestrial, aerial present}} = 0.264$; $R^2_{\text{terrestrial, terrestrial present}} = 0.297$; $R^2_{\text{aerial, terrestrial present}} = 0.336$; $R^2_{\text{aerial, aerial present}} = 0.340$) suggesting that changes in these parameters act primarily by relaxing selection for recognition abilities.

escape. And, the cost of escape interacted with mutation rate because if the mutation rate was relatively low, escape costs should become relatively more important in explaining the persistence of predator recognition abilities.

We simulated predator lethality by varying the speed of the predators. The effects of differential predator lethality varied depending upon the presence of predators. When we analysed the effect of any predator present, differential predator lethality explained variation only in aerial predator recognition. When we examined the effects of the presence of specific predators, we found variation in differential lethality had its effects on recognition abilities for the specific predator present. Thus, variation in lethality influenced aerial predator recognition abilities when aerial predators were present, and terrestrial predator recognition abilities when terrestrial predators were present.

While the presence of predators was not the most important factor explaining persistence of predator recognition abilities, the way in which the presence of specific types of predators influenced both the average and standard deviation of terrestrial, but not aerial predator recognition lends some support for the multi-predator hypothesis. Specifically, the multi-predator hypothesis predicts linkage, and linkage would predict that the presence of one predator would affect recognition abilities for the predator not present. When terrestrial predators were present, aerial predator recognition abilities were greater and less variable, suggesting that the presence of terrestrial predators was sufficient to maintain antipredator behavior for aerial predators. This is the opposite of what was hypothesized to occur with tammar wallabies (Blumstein and Daniel, 2002), but nonetheless illustrates the potential importance of predators on the antipredator behavior for other predators.

In conclusion, we found that costs of maintaining antipredator behavior are relatively more important than the presence of predators in explaining variation in predator recognition abilities in a situation where predation risk was relaxed by removing predators. We also found that the presence of one predator can influence predator recognition abilities for a predator no longer present. Thus, our results provide some support for the multi-predator hypothesis.

In general, our results suggest that a deeper understanding of the costs of discrimination is essential to understand the conditions under which antipredator behavior persists. Identifying such costs will require comparisons of individuals with different evolutionary histories of predator exposure. Antipredator behavior often varies geographically, and researchers can capitalize on such variation (e.g. Foster, 1999; Krause and Ruxton, 2002; Beauchamp, 2004). Responses need not be innate (Griffin et al., 2000), and we know that experience with predators can rapidly restore antipredator behavior lost over evolutionary time (e.g. Hunter and Skinner, 1998; Berger et al., 2001; Laundré et al., 2001). In general, we might expect that the removal of a predator that selects for a high-cost response will have different effects on the persistence of antipredator behavior than the removal of a predator with a low-cost response. Over time, species are exposed to different types of predators, and populations are exposed to different subsets of predators (e.g. Reimchen, 1994). We might expect pleiotropy and/or linkage to evolve in situations where the costs of different traits are relatively equal.

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