Ethology

CURRENT ISSUES – PERSPECTIVES AND REVIEWS

# The Multipredator Hypothesis and the Evolutionary Persistence of Antipredator Behavior

Daniel T. Blumstein

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA

**Correspondence**
Daniel T. Blumstein, Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA.
E-mail: marmots@ucla.edu

Received: September 30, 2005
Initial acceptance: November 1, 2005
Final acceptance: November 11, 2005
(S. Forbes)

doi: 10.1111/j.1439-0310.2006.01209.x

**Invited Review**

## Abstract

Isolation from predators affects prey behavior, morphology, and life history, but there is tremendous variation in the time course of these responses. Previous hypotheses to explain this variation have limited predictive ability. I develop a 'multipredator' hypothesis to explain the evolutionary persistence of antipredator behavior after the loss of some, but not all, of a species' predators. The hypothesis assumes pleiotropy, whereby elements of antipredator behavior may function in non-predatory situations, and linkage, such that genes influencing the expression of antipredator behavior do not assort independently. The hypothesis is restricted to species with multiple predators (most species) and aims to predict the conditions under which antipredator behavior will persist following the loss of one or more of a species' predators. I acknowledge that the relative costs of non-functional antipredator behavior will influence the likelihood of linkage and therefore persistence. The hypothesis makes two main predictions. First, genes responsible for antipredator behavior will not be scattered throughout the genome but rather may be found close together on the same chromosome(s). Secondly, the presence of any predators may be sufficient to maintain antipredator behavior for missing predators. Advances in behavioral genetics will allow tests of the first prediction, while studies of geographic variation in antipredator behavior provide some support for the second.

## Introduction

Studies of geographic variation in behavior illustrate both remarkable plasticity and remarkable persistence when a population becomes isolated from predators (Diamond 1990; Berger 1998, 1999; Coss 1999; Magurran 1999; Berger et al. 2001). For instance, reduction in predation pressure allows animals to forage more and allocate less time to antipredator vigilance (e.g. Catterall et al. 1992; Hunter & Skinner 1998; Blumstein et al. 2001), be choosier when looking for mates (e.g. Forsgren 1992; Berglund 1993; Briggs et al. 1996), spend less time with others (Magurran & Seghers 1994), modify group sizes (Heard 1992), aggressively defend breeding territories (Huntingford 1982), or forage in other places (e.g. Werner et al. 1983; Bland & Temple 1990; Suhonen 1993). 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 & Houde 1995). However, some antipredator behavior persists for many thousands of years after isolation (Byers 1997; Coss 1999; Blumstein et al. 2000; Blumstein & Daniel 2002), and there is no adequate model to account for this variation.

## Existing Hypotheses to Explain Persistence

There are several inter-related hypotheses to explain the persistence of antipredator traits under relaxed selection; however, they act at different levels (Tinbergen 1963) of biological organization and are not necessarily mutually exclusive. All assume some degree of heritable variation in antipredator behavior (e.g. Seghers 1974; Magurran 1990; Riechert & Hedrick 1990). Much antipredator behavior requires some experience for proper performance (Griffin et al. 2000), and I acknowledge that mechanisms of antipredator behavior can influence the phenotypic response to isolation from predators (Blumstein 2002). Specifically, relatively hard-wired traits will have evolutionary responses, while relatively experience-dependent traits will have an immediate response to the loss of experience with predators. However, hypotheses that explain the evolutionary response to relaxed selection treat experience as an obscuring variable (i.e. it increases phenotypic variation).

The 'ghost of predators past' hypothesis (Peckarsky & Penton 1988; Byers 1997) simply says that a species subject to past selection for antipredator behavior will retain antipredator behavior if it is not too costly to do so (e.g. Neill 1990). This hypothesis, while descriptive, does not enable us to explain variation in how different species and populations within a species respond to relaxed selection without specific knowledge of selection differentials (i.e. differential costs) and heritability estimates (Falconer 1981). However, it does highlight the importance of costs, which will be developed further below.

Darwin (1859) recognized that vestigial structures will become more variable after selection is relaxed because they are no longer checked by natural selection. Haldane (1933) noted that mutations will accumulate on non-selected traits causing an increase in variation. Decay (Coss 1999) of non-selected traits is not inevitable, however, and is less likely for traits with pleiotropic effects (Byers 1997).

A second hypothesis suggests that antipredator behavioral traits have pleiotropic effects on other traits, which will be functional regardless of the presence or absence of predators (Byers 1997; Coss 1999). At the genomic level proteins that are centrally located in networks (Hahn & Kern 2004) are buffered from change, and this centrality may provide a mechanism by which pleiotropy may constrain the rate of evolutionary change. Pleiotropy occurs at higher levels of organization as well. For instance, local guidance molecules are used for both axonal and dendritic organization (Kim & Chiba 2004), and the same genes are responsible for the organization of the visual cortex and the thalamus (Sestan et al. 2001). For all of these reasons, pleiotropy seems to be a reasonable mechanism explaining persistence. Unfortunately, without detailed knowledge of behavioral genetics (e.g. Brodie 1989), the 'pleiotropic' hypothesis does not enable us to predict how a given species or population will respond to relaxed or modified selection.

A third, but related, hypothesis focuses on the specific type of antipredator behavior and the degree to which it is 'functionally integrated' with other behaviors (Coss 1999). At the genomic level we know that overlapping gene function slows the evolutionary rates of specific genes and prevents mutational loss (Wagner 2000). And, specific and novel adaptations are likely to respond quickly to loss-of-function (Curio 1993; Biardi et al. 2000, 2005). Antipredator behavior varies in its specialization and uniqueness (Caro 2005). Some less specialized antipredator behavior has components used for other non-antipredator activities. For instance, vigilance has social (Roberts 1988) and antipredator functions (Lima & Dill 1990) and we might not expect animals to stop looking around if there are suddenly no predators. Alternatively, a specialized antipredator adaptation may no longer have a benefit following isolation and will be lost if there is any cost (Cruz & Wiley 1989; Magurran 1999). The 'specialization' hypothesis predicts that specialized and less functionally integrated antipredator behavior will be the first to be lost following isolation. In practice, however, it is difficult to rank behaviors with respect to their specialization or functional integration.

## The Multipredator Hypothesis

Here, I developed an integrated hypothesis that incorporates components from the previous hypotheses. Because these act at different levels of biological organization, all may be viewed as relating to a central hypothesis: that shared systems may be buffered from change at the genomic, epigenetic, and functional level of behavioral expression. I assume that antipredator behavior has pleiotropic effects and that behaviors may be genetically linked (see below). I acknowledge that prey have more than a single species of predator and a suite of antipredator adaptations. Many studies of the evolutionary response of antipredator behavior to relaxed selection have considered only the loss of a single, presumably important, predator. However, recent theory suggests that the picture is much more complex when multiple predator species are considered (Lima 1992, 2002; Sih et al. 1998; Krams 2000). For instance, small mammals commonly must avoid being killed by raptors, carnivorous mammals, and reptiles. Avoiding different predators may require predator-specific strategies (e.g. Owings & Coss 1977; Cheney & Seyfarth 1990; Bouskila 1995; Caro 2005). Thus, when desert rodents remain close to cover on moonlit nights they will avoid raptor predation, but the risk of snake predation may be moonlight independent (Bouskila 1995).

All antipredator behavior shares some common physiological and behavioral mechanisms. Consider vertebrates that respond to predators by escape. To avoid a predator, individuals must be able to become physiologically aroused – they must have a fear response (e.g. Blanchard et al. 1989, 1990). They must also allocate some time to antipredator vigilance. Such inter-related behavioral mechanisms (sensu Coss 1999) should be resistant to the loss of a single predator because both physiologic arousal and vigilance may have other functions.

Antipredator behavior, while often species specific, should not be expected to evolve independently. Antipredator behavior commonly involves an individual first identifying a predator, and then responding in some way. If there are common cues shared among predators (e.g. if predatory raptors have similar silhouettes), then we expect an integrated raptor recognition system (sensu Curio 1973). In this case, the removal of a single raptor should have limited effect on the persistence of the system. Alternatively, some traits may be evolutionary fragile (such as the recognition of the shrike eye band by pied flycatchers; Curio 1993). The multipredator hypothesis goes beyond simply predicting that specifically shared antipredator responses (e.g. raptor recognition) will be buffered from the loss of a single species of raptor, it suggests a deeper level of integration brought about by linkage.

We should expect traits that function together to be linked. For instance, animal homeodomain (HOM/*Hox* genes) are responsible for the variety of traits that determine anterioposterior axial development (Purugganan 1998; Halanych & Passamaneck 2001). These genes are remarkably conserved among phyla and have evolved into clusters along chromosomes (Cohn 2002). Similarly, we see tight linkage (whereby genes responsible for parts of a process are located next to each other) in physiologically important genes such as the lac operon, which codes for proteins involved in lactose metabolism.

Avoiding predation is something that virtually all animals must do and there has been a long history of selection for antipredator behavior in all phyla. Thus, we might expect similar genomic architecture underlying the genetic basis of antipredator behavior. Consider an ungulate which, when born, reduces predation risk by combining its crypsis with immobility. If these traits evolved independently, individuals with one but not both of them would be at a selective disadvantage. It is also possible to envision more complex relationships between antipredator behaviors. Chickens (*Gallus gallus*) and other galliforms commonly avoid predation by raptors by crouching and freezing after they detect a raptor, yet have a more active response to terrestrial predators (Evans et al. 1993). Individuals with one, but not both, appropriate responses would be at a selective disadvantage. We might therefore expect loci responsible for these responses to be linked.

Fisher (1958) first suggested that complex traits would be relatively resistant to mutational change because mutations are less likely to be favorable in a complex organism than in a simple one. More recently, Orr (2000) demonstrated that this mutational cost is much larger than Fisher assumed. Thus, complex antipredator behavior may be buffered from change. A potential cost of such complexity, however, is degenerative change in the absence of any selection. Pleiotropy may provide the necessary selection to maintain complex traits.

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. Thus, the presence of a single predator should maintain antipredator adaptations for predators no longer present.

## A Caveat: the Relative Costs to Maintaining No Longer Functional Behavior will Influence the Likelihood of Linkage and the Likelihood of Persistence Under Relaxed Selection

Imagine a linked complex of three different predator-specific antipredator traits, A, B, and C. Assume the benefits associated with their proper performance is identical; when properly used they reduce predation risk. However, each will have a cost that emerges in the absence of the predator for which it evolved. For instance, galliforms are often immobile after detecting a raptor (Evans et al. 1993). If there are no raptors, but an individual falsely identifies a raptor (i.e. a Type II error), it will, by freezing, experience a lost opportunity cost. Suppressing foraging for a few minutes while responding to a non-existent predator may not substantially reduce fitness. However, costs may be more extreme than a simple lost opportunity cost. Many species have metabolically expensive protective body armor in areas with predators (e.g. sticklebacks, *Gasterosteus aculeatus* – Reimchen 1994). By investing in armor, animals allocate energy that could be otherwise used for reproduction and we know that the loss of picivorous fish, but not the loss of picivorous birds leads to the rapid loss of protective armor (Reimchen 1994). Thus, there are clear differences in the costs of missed opportunities (most of which are likely to be relatively small) compared with the costs of maintaining armor in a predator-free location (which directly affects reproductive success). These costs should influence the likelihood of pleiotropy and/or linkage, and therefore the likelihood of antipredator adaptations persisting after the removal of one or more predators.

Assume that A and B have identical costs (e.g. missed opportunity or other time costs), but C is much more costly (e.g. body armor). The removal of the predator that has selected for behavior C will make the maintenance of behavior C extremely costly. Thus, we might not expect that costly traits will be incorporated into co-evolved complexes of antipredator behavior.

More generally, the removal of a predator that selects for a high-cost response will have different effects 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. We might also generally expect behavioral traits to co-evolve whereas more costly, and less plastic, morphological and life-history traits might evolve independently.

## Testing the Multipredator Hypothesis

The multipredator hypothesis makes predictions about genomic design and predictions about how populations will respond to the loss of some vs. all of their predators. First, genes responsible for antipredator behavior will not be scattered throughout the genome. It is likely that traits of equal cost will be found together for selection should break apart linkages for traits that impose high costs in the absence of predators. Secondly, the presence of any predators may be sufficient to maintain antipredator behavior for missing predators. Advances in behavioral genetics and functional genomics will allow tests of the first prediction, while studies of geographic variation in antipredator behavior have allowed tests of the second.

## Preliminary Support for the Multipredator Hypothesis

Kangaroos and wallabies are found in locations with different histories of exposure to predators (Blumstein 2002). Western grey kangaroos (*Macropus fuliginosus*) isolated from all predators for approx. 9500 yr on Kangaroo Island, South Australia, lost group size effects – the systematic change in time allocated to vigilance and foraging as a function of group size (Blumstein & Daniel 2002). By contrast, tammar wallabies (*Macropus eugenii*) isolated from terrestrial predators on Kangaroo island, but not from aerial predators, retained group size effects (Blumstein & Daniel 2002). This result could be explained by the presence of raptors on Kangaroo Island maintaining a heightened state of nighttime readiness in the wallabies. Such perceptual priming is seen in other antipredator systems (e.g. snake-naïve squirrels monkeys, *Saimiri sciureus*, respond fearfully to snakes only when reared with live food – Masataka 1993, and with humans suffering post-traumatic stress may re-experience the traumatic situation in different contexts – Ehlers & Clark 2000), and suggests a proximate mechanism underlying the responds to wallabies without mammalian predators.

Further support for the multipredator hypothesis comes from a study of tammar wallabies isolated from all predators for as few as 130 yr in New Zealand, which lost antipredator behaviors that were seen in populations exposed to some risk of predation (Blumstein et al. 2004). Specifically, predator discrimination abilities degraded (cf. Blumstein et al. 2004 with Blumstein et al. 2000), and group size effects were lost. Intriguingly, a recent finding suggests that the presence of group size effects may be more influenced by being isolated on islands than by predators, per se (Blumstein & Daniel 2005). Insularity effects are consistent both with the idea that founder effects may have a substantial influence on the presence of antipredator behavior, as well as the idea that the relative costs of maintaining certain behaviors is influenced by living on islands. Future empirical work is needed to tease these different causal factors apart.

An agent-based simulation modeled after the kangaroo and wallaby system allowed the study of the effect of the presence of one predator on antipredator recognition for another, no longer present predator. Results documented asymmetric responses whereby, terrestrial predator recognition was influenced by the presence of terrestrial predators, but the presence of aerial predator recognition was neither influenced by the presence of aerial predators, nor the presence of terrestrial predators (Blumstein et al. 2005). This finding of asymmetric responses is consistent with the multipredator hypothesis. Results also revealed that escape costs are more important than the presence of predators in explaining the persistence of antipredator behavior: expensive traits are likely to be lost quickly, a finding consistent with the caveat about costs described above.

Examining other reports of evolutionary persistence in light of the multipredator hypotheses provides further support for the importance of species encountering any predators. A great deal is known about the evolutionary persistence of rattlesnake (*Crotalus* spp.) recognition in California ground squirrels (*Spermophilus beecheyi*) (reviewed in Coss & Goldthwaite 1995; Coss 1999). Studies of a number of populations have suggested that rattlesnake recognition abilities can be maintained for >70,000 yr after isolation from rattlesnakes. While anti-snake behavior (prolonged investigation) is very different from the antipredator behavior elicited by birds and mammals (flee to burrow), the multipredator hypothesis would suggest that the remarkable persistence of anti-snake behavior results from California ground squirrels encountering a variety of other mammalian and avian predators along with a less-threatening snake.

Galápagos finches (*Geospiza* spp.) retain responsiveness to snakes and raptors, but the overall level of responsiveness may be attenuated on islands without a specific predator (Curio 1966). Finches on a predator-free island also retained rudimentary responses, but it is neither clear when these finches colonized the island (Coss 1999), nor what the costs of these rudimentary responses are. Traits will only be lost if there is some cost to their maintenance (or due to chance events not selected against), but loss may take some time, and variable responses are expected (e.g. Darwin 1859).

North American pronghorn antelope (*Antilocapra americana*) retain a number of antipredator behaviors (including their relatively fast sprint speeds) that are presumably adaptive for dealing with large cursorial predators that went extinct in the Pleistocene (Byers 1997). However, while apparently uncommon, mammalian predators (Byers 1997), and presumably golden eagles (*Aquila chrysaetos*) still prey upon adult and young pronghorn. Thus, it may not be surprising that antipredator behavior persists despite the loss of historically important predators.

The multipredator hypothesis assumes that the underlying genetic basis of antipredator behavior has, by pleiotropy or linkage, become a functional package. While the arguments are logically sound, precise genetic evidence is lacking. Evidence from quantitative genetics suggests that many traits do not evolve independently. For instance, in one of the best-studied natural systems, a number of guppy traits covary with predation risk (Endler 1995). However, there are several ways that this phenotypic covariation can arise, and it is premature to say whether these phenotypic correlations represent an underlying genetic covariance (Rausher 1992), or simply reflects underlying environmental covariation (e.g. Rausher 1992; Endler 1995). Quantitative genetic studies tell us that there may be genetic correlations, but we currently do not know the precise degree to which different components of antipredator behavior are linked (McMillian et al. 2002). At this point the assumption of coevolving packages of antipredator behavior on which the multipredator hypothesis acts must remain a testable hypothesis.

## Broader Implications of the Multipredator Hypothesis

The multipredator hypothesis may be particularly useful to those interested in predicting how species would respond to encountering predators after a period of relaxed selection. Such encounters may be natural, as seen during range expansions or result from translocations – the moving of animals from one location to another, and reintroductions – the movement of animals from captivity to the wild (Kleiman 1989). Translocations and reintroductions are two important tools for conservation, but most fail (Wolf et al. 1996; Fischer & Lindenmayer 2000) and predation is often involved in their failure (Beck et al. 1991; Short et al. 1992; Miller et al. 1994). Predator-naïve animals may be given pre-release experience with predators (Griffin et al. 2000, 2001) that may increase survival (van Heezik et al. 1999). However, evolutionarily unprepared species will likely not benefit from such training (Griffin et al. 2000). The key factor is likely to be prior experience with any predators. Additionally, species are routinely moved around the Earth by humans (Low 1999), and global climate change is modifying species distributions (e.g. Burgman & Lindenmayer 1998; Davis & Shaw 2001). To predict how species that suddenly encounter predators may respond, some knowledge of past exposure to predators is needed. Species with historical exposure to predators may fare better than those with no exposure, although the introduction of completely novel predators (e.g. humans: Martin 1984; red foxes: Short et al. 2002) might pose additional unique problems.

The 'overkill' or 'blitzkreig' hypothesis (e.g. Martin 1963, 1984; Diamond 1989) to explain the extinction of mega-herbivores upon encountering humans assumes that species such as moas on New Zealand, mammoths and mastodons in North America, and large kangaroos in Australia were predator naïve and had no flight response to humans (e.g. Flannery 1994, 2001). However, the multipredator hypothesis would predict that continental species would not be entirely predator-naïve because they evolved with a remarkable variety of avian, mammalian, and in some cases reptilian predators (e.g. Wroe 1999; Flannery 2001; Wroe et al. 2002, 2004). Rather than having a continent of fearless animals waiting to be killed by an advancing wave of hunters (e.g. Flannery 2001), it is more likely that human hunters posed unique threats, and that while not entirely predator-naïve, the hunted animals did not have sufficient antipredator behavior to cope with these unique threats. Similar extinctions of Australian mammals following the introduction of the red fox may not have resulted from Australian mammals being entirely predator naïve, but rather because foxes have novel hunting behavior (e.g. they may engage in surplus killing – i.e. kill more than it can eat at a single sitting – Short et al. 2002). Thus, the lessons from blitzkrieg models may explain human proficiency in eradicating species, but may not be generalizable to more 'natural' processes following range expansions or the processes that follow re-introductions for conservation.

## Acknowledgements

Conversations with, and comments by, Peter Bednekoff, Joel Berger, Nancy Burley, Janice Daniel, Katy Semple Delaney, John Endler, Greg Grether, Jim Hare, Dave Jacobs, Gita Kolluru, Steve Wroe, and especially Peter Nonacs (who emphasized the importance of considering relative costs), and Dick Coss (who emphasized that evolutionary persistence results from shared system properties at different levels of organization) have helped improve my presentation of the multipredator hypothesis.

## Literature Cited

Beck, B. B., Kleiman, D. G., Dietz, J. M., Castro, I., Carvalho, C., Martins, A. & Rettberg-Beck, B. 1991: Losses and reproduction in reintroduced golden lion tamarins *Leontopithecus rosalia*. Dodo J. Jersey Wild. Preserv. Trust **27**, 50—61.

Berger, J. 1998: Future prey: some consequences of the loss and restoration of large carnivores. In: Behavioral Ecology and Conservation Biology (Caro, T. M. ed.). Oxford Univ. Press, New York, pp. 80—100.

Berger, J. 1999: Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. Proc. R. Soc. Lond. B **266**, 2261—2267.

Berger, J., Swenson, J. E. & Persson, I.-L. 2001: Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. Science **291**, 1036—1039.

Berglund, A. 1993: Risky sex: male pipefishes mate at random in the presence of a predator. Anim. Behav. **46**, 169—175.

Biardi, J. E., Coss, R. G. & Smith, D. G. 2000: California ground squirrel (*Spermophilus beecheyi*) blood sera inhibits crotalid venom proteolytic activity. Toxicon **38**, 713—721.

Biardi, J. E., Chien, D. C. & Coss, R. G. 2005: California ground squirrel (*Spermophilus beecheyi*) defenses against rattlesnake venom digestive and hemostatic toxins. J. Chem. Ecol. **31**, 2501—2518.

Blanchard, R. J., Blanchard, D. C. & Hori, K. 1989: An ethoexperimental approach to the study of defense. In: Ethoexperimental Approaches to the Study of Behavior (Blanchard, R. J., Bain, P. F., Blanchard, D. C. & Parmigiani, S. eds). Kluwer Academic Publishers, Dordrecht, pp. 114—136.

Blanchard, D. C., Blanchard, R. J. & Rodgers, R. J. 1990: Pharmacological and neural control of anti-predator defense in the rat. Aggress. Behav. **16**, 165—175.

Bland, J. D. & Temple, S. A. 1990: Effects of predation-risk on habitat use by Himalayan Snowcocks. Oecologia **82**, 187—191.

Blumstein, D. T. 2002: Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. J. Biogeogr. **29**, 685—692.

Blumstein, D. T. & Daniel, J. C. 2002: Isolation from mammalian predators differentially affects two congeners. Behav. Ecol. **13**, 657—663.

Blumstein, D. T. & Daniel, J. C. 2005: The loss of anti-predator behaviour following isolation on islands. Proc. R. Soc. Ser. B **272**, 1663—1668.

Blumstein, D. T., Daniel, J. C., Griffin, A. S. & Evans, C. S. 2000: Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. Behav. Ecol. **11**, 528—535.

Blumstein, D. T., Daniel, J. C. & McLean, I. G. 2001: Group size effects in quokkas. Aust. J. Zool. **49**, 641—649.

Blumstein, D. T., Daniel, J. C. & Springett, B. P. 2004: A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. Ethology **110**, 919—934.

Blumstein, D. T., Bitton, A. & Da Veiga, J. 2005: How does the presence of predators influence the persistence of antipredator behavior?. J. Theor. Biol. doi:10.1016/j.jtbi.2005.08.011.

Bouskila, A. 1995: Interactions between predation risk and competition: a field study of kangaroo rats and snakes. Ecology **76**, 165—178.

Briggs, S. E., Godin, J. G. J. & Dugatkin, L. A. 1996: Mate-choice copying under predation risk in the Trinidadian guppy (*Poecila reticulata*). Behav. Ecol. **7**, 151—157.

Brodie, E. D. III, 1989: Genetic correlations between morphology and antipredator behaviour in natural populations of the garter snake *Thamnophis ordinoides*. Nature **342**, 542—543.

Burgman, M. A. & Lindenmayer, D. B. 1998: Conservation Biology for the Australian Environment. Surrey Beatty and Sons, Chipping Norton, NSW.

Byers, J. A. 1997: American Pronghorn: Social Adaptations and the Ghosts of Predators Past. Univ. Chicago Press, Chicago, IL.

Caro, T. 2005: Antipredator Defenses in Birds and Mammals. Univ. of Chicago Press, Chicago, IL.

Catterall, C. P., Elgar, M. A. & Kikkawa, J. 1992: Vigilance does not covary with group size in an island population of silvereyes (*Zosterops lateralis*). Behav. Ecol. **3**, 207—210.

Cheney, D. L. & Seyfarth, R. M. 1990: How Monkeys See the World. Univ. of Chicago Press, Chicago, IL.

Cohn, M. J. 2002: *Hox* genes. In: Encyclopedia of Evolution (Pagel, M. ed.). Oxford Univ. Press, New York, pp. 506—510.

Coss, R. G. 1999: Effects of relaxed natural selection on the evolution of behavior. In: Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms (Foster, S. A. & Endler, J. A. eds). Oxford Univ. Press, Oxford, pp. 180—208.

Coss, R. G. & Goldthwaite, R. O. 1995: The persistence of old designs for perception. Persp. Ethol. **11**, 83—148.

Cruz, A. & Wiley, J. W. 1989: The decline of an adaptation in the absence of a presumed selection pressure. Evolution **43**, 55—62.

Curio, E. 1966: How finches react to predators. Animals **9**, 142—143.

Curio, E. 1973: Towards a methodology of teleonomy. Experientia **29**, 1045—1058.

Curio, E. 1993: Proximate and developmental aspects of antipredator behavior. Adv. Study Behav. **22**, 135—238.

Darwin, C. 1859: On the Origin of Species by Means of Natural Selection or the Preservation of Favored Races in the Struggle for Life. Murray, London.

Davis, M. B. & Shaw, R. G. 2001: Range shifts and adaptive responses to quaternary climate change. Science **292**, 673—679.

Diamond, J. M. 1989: The present, past and future of human-caused extinctions. Philos. Trans. R. Soc. Lond. B **325**, 469—477.

Diamond, J. 1990: Biological effects of ghosts. Nature **345**, 769—770.

Ehlers, A. & Clark, D.M. 2000: A cognitive model of posttraumatic stress disorder. Behav. Res. Ther. **38**, 319—345.

Endler, J. A. 1980: Natural selection on color patterns in *Poecilia reticulata*. Evolution **34**, 76—91.

Endler, J. A. 1995: Multiple-trait coevolution and environmental gradients in guppies. Trends Ecol. Evol. **10**, 22—29.

Endler, J. A. & Houde, A. E. 1995: Geographic variation in female preferences for male traits in *Poecilia reticulata*. Evolution **49**, 456—468.

Evans, C. S., Evans, L. & Marler, P. 1993: On the meaning of alarm calls: functional reference in an avian vocal system. Anim. Behav. **46**, 23—38.

Falconer, D. S. 1981: Introduction to Quantitative Genetics, 2nd edn. The Pitman Press, Bath, UK.

Fischer, J. & Lindenmayer, D. B. 2000: An assessment of the published results of animal relocations. Biol. Conserv. **96**, 1—11.

Fisher, R. A. 1958: The Genetical Theory of Natural Selection. Dover Publications Inc., New York.

Flannery, T. F. 1994: The Future Eaters. Reed Books, Port Melbourne.

Flannery, T. 2001: The Eternal Frontier. Text Publishing, Melbourne.

Forsgren, E. 1992: Predation risk affects mate choice in a gobiid fish. Am. Nat. **140**, 1041—1049.

Griffin, A. S., Blumstein, D. T. & Evans, C. S. 2000: Training captive-bred or translocated animals to avoid predators. Conserv. Biol. **14**, 1317—1326.

Griffin, A. S., Evans, C. S. & Blumstein, D. T. 2001: Learning specificity in acquired predator recognition. Anim. Behav. **62**, 577—589.

Hahn, M. W. & Kern, A. D. 2004: Comparative genomics of centrality and essentiality in three eukaryotic protein-interaction networks. Mol. Biol. Evol. **22**, 803—806.

Halanych, K. M. & Passamaneck, Y. 2001: A brief review of Metazoan phylogeny and future prospects in Hox-research. Am. Zool. **41**, 629—639.

Haldane, J. B. S. 1933: The part played by recurrent mutation in evolution. Am. Nat. **67**, 5—19.

Heard, D. C. 1992: The effect of wolf predation and snow cover on musk-ox group size. Am. Nat. **139**, 190—204.

van Heezik, Y., Seddon, P. J. & Maloney, R. F. 1999: Helping reintroduced houbara bustards avoid predation: effective anti-predator training and the predictive value of pre-release behaviour. Anim. Conserv. **2**, 155—163.

Hunter, L. T. B. & Skinner, J. D. 1998: Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour **135**, 195—211.

Huntingford, F. A. 1982: Do inter- and intra-specific aggression vary in relation to predation pressure in sticklebacks?. Anim. Behav. **30**, 909—916.

Kim, S. & Chiba, A. 2004: Dendritic guidance. Trends Neurosci. **27**, 194—202.

Kleiman, D. G. 1989: Reintroduction of captive mammals for conservation: guidelines for reintroducing endangered species into the wild. BioSci. **39**, 152—161.

Krams, I. 2000: Length of feeding day and body weight of great tits in a single- and a two-predator environment. Behav. Ecol. Sociobiol. **48**, 147—153.

Lima, S. L. 1992: Life in a multi-predator environment: some considerations for anti-predatory vigilance. Ann. Zool. Fenn. **29**, 217—226.

Lima, S. L. 2002: Putting predators back into behavioral predator-prey interactions. Trends Ecol. Evol. **17**, 70—75.

Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**, 619—640.

Low, T. 1999: Feral Future. Viking, Ringwood, Victoria.

Magurran, A. E. 1990: The inheritance and development of minnow anti-predator behaviour. Anim. Behav. **39**, 834—842.

Magurran, A. E. 1999: The causes and consequences of geographic variation in antipredator behavior: perspectives from fish populations. In: Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms (Foster, S. A. & Endler, J. A. eds). Oxford Univ. Press, New York, pp. 139—163.

Magurran, A. E. & Seghers, B. H. 1994: Predator inspection behaviour covaries with schooling tendency amongst wild guppy, *Poecilia reticulata*, populations in Trinidad. Behaviour **128**, 121—134.

Martin, P. S. 1963: Prehistoric overkill. In: Pleistocene Extinctions: the Search for a Cause (Martin, P. S. & Wright, H. E., eds). Yale Univ. Press, New Haven, CT, pp. 75—120.

Martin, P. S. 1984: Pleistocene overkill: the global model. In: Quaternary Extinctions: a Prehistoric Revolution (Martin, P. S. & Klein, R. G. eds). Univ. of Arizona Press, Tucson, AZ, pp. 354—403.

Masataka, N. 1993: Effects of experience with live insects on the development of fear of snakes and squirrels monkeys, *Saimiri sciureus*. Anim. Behav. **46**, 741—746.

McMillian, W. O., Monteiro, A. & Kapan, D. D. 2002: Development and evolution on the wing. Trends Ecol. Evol. **17**, 125—133.

Miller, B., Biggins, D., Hanebury, L. & Vargas, A. 1994: Reintroduction of the black-footed ferret (*Mustela nigripes*). In: Creative Conservation: Interactive Management of Wild and Captive Animals (Olney, P. J. S., Mace, G. M. & Feistner, A. T. C. eds). Chapman and Hall, London, pp. 455—464.

Neill, W. E. 1990: Induced vertical migration in copepods as a defense against invertebrate predation. Nature **345**, 524—526.

Orr, H. A. 2000: Adaptation and the cost of complexity. Evolution **54**, 13—20.

Owings, D. H. & Coss, R. G. 1977: Snake mobbing by California ground squirrels: adaptive variation and ontogeny. Behaviour **62**, 50—68.

Peckarsky, B. L. & Penton, M. A. 1988: Why do Ephemerella nymphs scorpion posture: a ''ghost of predation past''? Oikos **53**, 185—193.

Purugganan, M. D. 1998: The molecular evolution of development. Bioessays **20**, 700—711.

Rausher, M. D. 1992: Natural selection and the evolution of plant-insect interactions. In: Evolutionary Perspectives on the Chemical Ecology of Insects (Roitberg, B. D. & Isman, M. B. eds). Chapman and Hall, London, pp. 20—88.

Reimchen, T. E. 1994: Predators and morphological evolution in threespine stickleback. In: The Evolutionary Biology of the Threespine Stickleback (Bell, M. A. & Foster, S. A. eds). Oxford Univ. Press, Oxford, pp. 240—276.

Riechert, S. E. & Hedrick, A. V. 1990: Levels of predation and genetically based anti-predator behaviour in the spider, *Agelenopsis aperta*. Anim. Behav. **40**, 679—687.

Roberts, S. C. 1988: Social influences on vigilance in rabbits. Anim. Behav. **36**, 905—913.

Seghers, B. H. 1974: Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary response to predation. Evolution **28**, 486—489.

Sestan, N., Rakic, P. & Donoghue, M. J. 2001: Independent parcellation of the embryonic visual cortex and thalamus revealed by combinatorial *Eph/ephrin* gene expression. Curr. Biol. **11**, 39—43.

Short, J., Bradshaw, S. D., Giles, J., Prince, R. I. T. & Wilson, G. R. 1992: Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia – a review. Biol. Conserv. **62**, 189—204.

Short, J., Kinnear, J. E. & Robley, A. 2002: Surplus killing by introduced predators in Australia – evidence for ineffective anti-predator adaptations in native prey species?. Biol. Conserv. **103**, 283—301.

Sih, A., Englund, G. & Wooster, D. 1998: Emergent impacts of multiple predators on prey. Trends Ecol. Evol. **13**, 350—355.

Suhonen, J. 1993: Predation risk influences the use of foraging sites by tits. Ecology **74**, 1197—1203.

Tinbergen, N. 1963: On aims and methods of ethology. Z. Tierpsychol. **20**, 410—433.

Wagner, A. 2000: The role of population size, pleiotropy and fitness effects of mutations in the evolution of overlapping gene function. Genetics **154**, 1389—1401.

Werner, E. E., Gilliam, J. F., Hall, D. J. & Mittelbach, G. G. 1983: An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**, 1540—1548.

Wolf, C. M., Griffith, B., Reed, C. & Temple, S. A. 1996: Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conserv. Biol. **10**, 1142—1154.

Wroe, S. 1999: Killer kangaroos and other murderous marsupials. Sci. Am. **280**, 68—74.

Wroe, S., Field, J. & Fullagar, R. 2002: Lost giants. Nat. Australia **27**, 54—61.

Wroe, S., Field, J., Fullagar, R. & Jermiin, L. S. 2004: Megafaunal extinction in the late quaternary and the global overkill hypothesis. Alcheringa **28**, 291—331.