UNDERSTANDING ANTIPREDATOR BEHAVIOR FOR CONSERVATION

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The sounds of the Australian night have changed since European settlement. Where the bilby (*Macrotis spp.*) once snuffled along poking its nose into the ground sniffing out invertebrates, and wallabies (Family Macropodidae) hopped along their pads commuting from their day beds in the scrub to their evening grassland foraging grounds, rabbit warrens are now a pox on the landscape, goats devour the cover so essential for native mammal shelters, and the ever-present foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) eat anything they can find. The last two centuries have not been kind to Australia's endemic fauna; 19 small and mid-sized marsupials and native rodents have gone extinct (Burgman and Lindenmayer 1998), and many more are either threatened or endangered. A combination of habitat clearing for agriculture, changed Aboriginal fire regimens, and the introduction of non-native herbivores (goats, sheep, cattle, buffalo, horses, donkeys, camels, and pigs) and predators (red foxes were introduced for hunting, and cats came along with European sailors and settlers) is implicated as the ultimate cause of native mammalian declines and extinctions (Johnson et al. 1989; Flannery 1994). Australia's ecology is seriously out of balance. While traditional "guns and poison" approaches to conservation may have their place in Australia (see Morris et al. 1998), in this essay I would like to illustrate how knowledge of animal behavior might also be useful in solving some of its conservation problems. More generally, I will review why all conservation biologists should think more critically about the evolution and adaptive significance of behavior.

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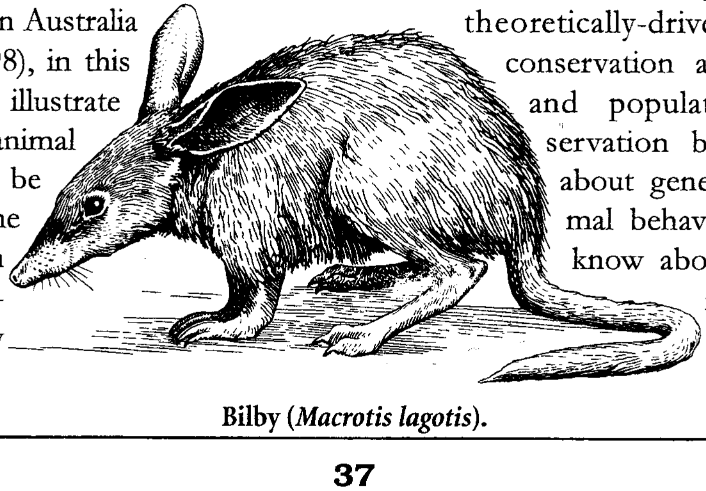
Conservation biologists, of course, often think of animal behavior. There is a growing literature documenting an increasing success of translocations and reintroductions to recover extinct populations. A consistent feature of this literature is its focus on individuals and on the consequences of behavioral development for subsequent survival (e. g., Miller et al. 1994; Badridze 1996; Pazhetnov 1996; Strijbosch 2000). Some researchers acknowledge that it is important to understand animal behavior, but view this knowledge as an expensive luxury for cash-strapped conservation biologists who should presumably allocate funds for habitat preservation. On the other hand, many conservation biologists remain naive in their understanding of animal behavior. If animals translocated from one place to another run, swim, crawl or fly away, it is thought of as a behavioral problem. Period. But such thinking trivializes the contribution of behavior to conservation.

A number of authors, including myself (Curio 1996; Clemmons and Buchholz 1997; Caro 1998; Anthony and Blumstein 2000; Gosling and Sutherland 2000), have argued that behavioral biology can make just as theoretically-driven contributions to conservation as population biology and population genetics. Conservation biologists must know about general principles of animal behavior just as they must know about population growth rates and inbreeding depression. To understand why, think about survival.



Bilby (*Macrotis lagotis*).

Whatever influences the probability that an individual survives over some time period determines a population's growth rate, size, and persistence time. Many factors influence survival and because it is individuals that live or die, these factors are ultimately behavioral. It is through behavior that individuals interact with their environment. Thus, understanding something about the ontogeny (Curio 1993), function (Roberts 1996), and diversity (Lima and Dill 1990) of antipredator behavior may help better manage wild populations and may help generate novel methods to conserve them.

By focusing on antipredator behavior I do not mean to ignore other behaviors because mate choice and mating systems, reproductive suppression, adaptive infanticide, dispersal, and habitat selection also may profoundly influence both survival and reproduction, and therefore also influence population size (e. g., Blumstein 1998, 2000; Anthony and Blumstein 2000 for a review). Rather, I focus here on antipredator behavior because it seems to be particularly important for Australian marsupial conservation.

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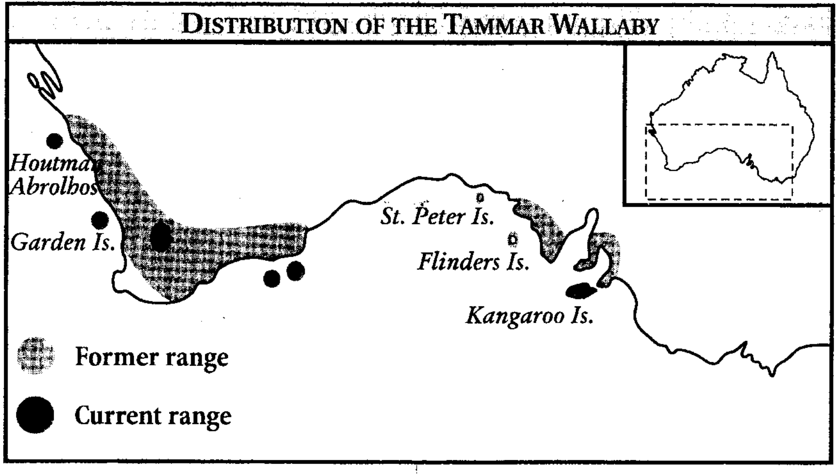
What happens when you move from a dangerous neighborhood to a safe one? Do you relax? Do you still lock your door and walk in well-lit areas? How long does it take you to relax? More importantly, what happens when you go back to the dangerous neighborhood? These are not irrelevant questions because many of the surviving Australian species have done just that. They are now found either on offshore islands without mammalian predators, or in fenced, predator-free reserves. Europeans introduced some species to offshore islands while other species have been naturally isolated on islands for the past 9,500 years by ice age-related sea level changes. These periods of isolation vary from several years — in the case of animals placed in fenced reserves or zoos, to a hundred or so years — in the case of some species placed onto offshore islands, to many thousands of years — in the case of those species or populations isolated since the last ice age. Understanding whether and how long antipredator behavior persists under relaxed selection is a key question for conservation biologists because it determines what antipredator abilities species possess (see also Berger 1999).

Because antipredator behavior must often be functional the first time an individual encounters a predator, it might initially seem odd that many species learn about their predators and that many antipredator behaviors depend on experience. But in many cases, and in a diversity of taxa, individuals require experience to properly perform antipredator behavior (Griffin et al. 2000). Having just said this, I will now point out that not all antipredator behavior is experience-dependent. Some behaviors persist for many thousands of years of relaxed selection.

For example, California ground squirrels (*Spermophilus beecheyi*) retain the ability to adaptively respond to poisonous rattlesnakes for up to 300,000 years after their populations have been isolated from them (Coss 1999). Extensive experiments by Coss and his colleagues (reviewed in Coss 1999) have determined that captive-born, predator-naive ground squirrels distinguish rattlesnakes from gopher snakes using a variety of acoustic, olfactory, and visual cues. Adult ground squirrels also have a well-developed resistance to rattlesnake venom. Geographically-isolated populations with different histories of exposure to snakes allowed the study of the evolutionary persistence of antipredator behavior under relaxed selection. It is interesting to note that physiological venom resistance in ground squirrels isolated from rattlesnakes dissipated within 9,000 years, while snake recognition abilities persisted for as many as 300,000 years.

My own work has shown that tammar wallabies (*Macropus eugenii*) — cat-sized, moderately social marsupials which, like other small macropodids, have experienced range reductions and local extinctions on the mainland following European settlement — retain the ability to recognize the sight of predators even after 9,500 years of isolation (Blumstein et al. 2000b). Wallabies on Kangaroo Island, South Australia evolved without their now-extinct marsupial predators because sea level changes had separated it from the mainland (Lampert 1979). Kangaroo Island was isolated before dingoes (*Canis lupus dingo*) were introduced to Australia (at least 3,500 years ago — Corbett 1995). Additionally, Kangaroo Island tammars have never been exposed to foxes which were introduced to the mainland about 130 years ago (Coman 1995). Yet, when tested in captivity, tammars appear to retain the ability to respond to the sight of a novel mammalian predator (red fox) by increasing their vigilance, and by foot-thumping (an alarm signal given by most macropodid marsupials), possibly because mammalian predators share convergent visual features.



DISTRIBUTION OF THE TAMMAR WALLABY

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Conservation managers must have some idea about which antipredator behaviors require learning before they reintroduce captively-bred animals to the wild, or before they translocate wild animals from predator-free areas to predator-rich areas. Most translocations and reintroductions for conservation fail (Wolf et al. 1996), and predation is often implicated as a key factor responsible for failure (Beck et al. 1991; Short et al. 1992; Miller et al. 1994). Fortunately, it seems that many species can be taught about the predators they are likely to encounter (McLean et al. 2000), and that the lessons they learn about one predator might be generalizable to other similar predators (Griffin et al. in review). Let me discuss these points in detail.

Ian McLean and his collaborators (McLean et al. 2000) have pioneered the process of training Australian marsupials (and New Zealand birds — McLean et al. 1999) to respond adaptively to predators which they previously showed little response to. By pairing the presentation of a model predator with an aversive stimulus, or by using a live, muzzled dog to act as both the model predator and the aversive stimulus, they taught rufous bettongs (*Aepyprymnus rufescens*), rufous hare-wallabies (*Lagorchestes hirsutus*), and quokkas (*Setonix brachyurus*) to respond fearfully or to produce a novel antipredator behavior (running to a refuge). Recent studies by our research group (Griffin et al. in review) have shown not only that tammar wallabies can be trained, but also that their training with one predator is generalizable to other similar predators. Specifically, tammars trained to increase their responsiveness to foxes also showed an increased response to cats (another potential predator), but not to non-predators (a conspecific and a goat). Moreover, prey required only a few training sessions to learn to fear novel predators. Thus, predator training may be a cost-effective way to help increase survival of potentially vulnerable prey by teaching them to respond specifically to predators. Finally, several other studies have demonstrated that predator training can increase the survival of reintroduced individuals (Ellis et al. 1977; van Heezik et al. 1999).

Not all species are appropriate for pre-release antipredator training. Ask anyone who has trained their dog, or ask a circus trainer; training works by enhancing pre-existing motor patterns. If a species (or a population) has been isolated for many generations and has lost the ability to exhibit any "behavioral precursors" that might be suitable for training, then the species or population will likely not benefit from training (Griffin et al. 2000). Before the Pleistocene extinctions, mainland Australia had a rich mammalian predator community containing thylacinids — marsupial lions/tigers, and dasyurids — quolls, tiger cats, and devils (Archer 1981; Robertshaw and Harden 1989), as well as raptors and large lizards. Thus, Australia's fauna should be particularly well-suited for pre-release predator training.

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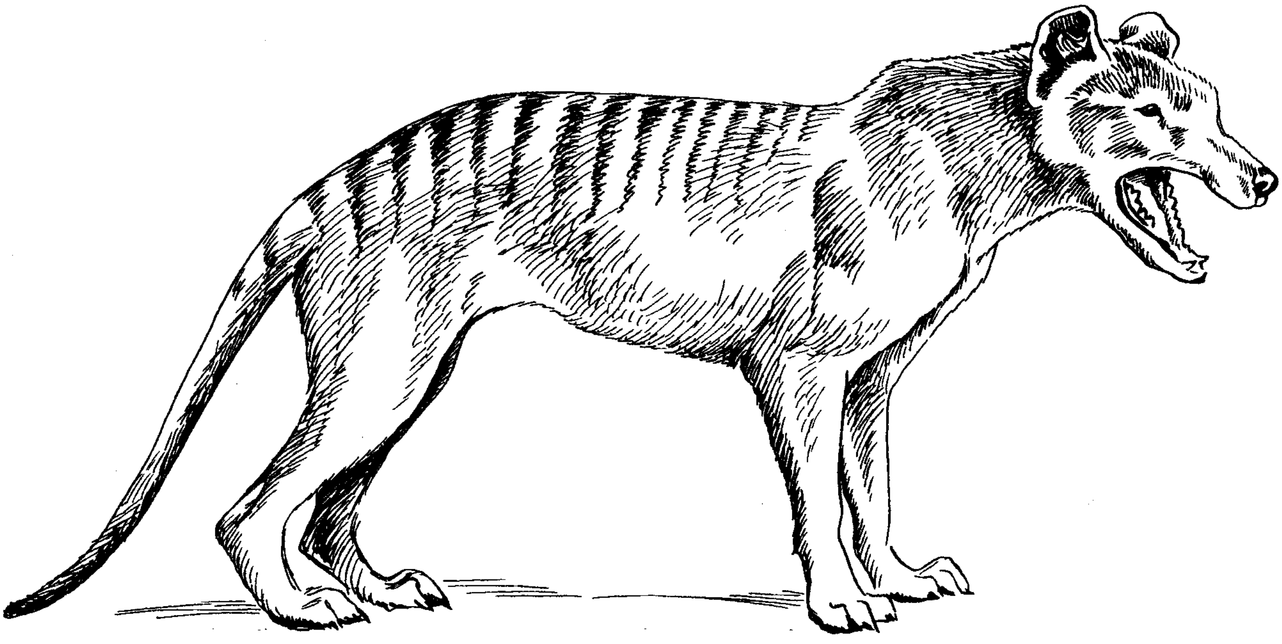
Translocations and reintroductions might also be more successful if managers considered more "hard-wired" antipredator behavior. Many species of mammals and birds modify the time they allocate to foraging and looking as a function of group size. Typically, animals in the open forage more and look less when in larger groups, a finding that is often attributed to a reduction in the per capita risk of predation as group size increases (Quenette, 1990). If so, animals benefit by having more eyes around to look for predators (Pulliam 1973) or by simply having other individuals available as an alternative food source for a hungry predator (Hamilton 1971).

Colleagues and I have discovered that the tammar wallaby, typically not considered very social because it shelters by day alone in dense cover and emerges at night to forage in open-membership aggregations, seems to benefit from associating with others (Blumstein et al. 1999). Theory predicts, and our tammar results illustrate, that the greatest benefits of aggregation occur with the addition of only a few individuals. By the time their aggregations reach eight to ten members, tammar wallabies are more or less unaffected by further increases in group size. Tammars in a group of ten are able to devote 16.5% more time to foraging, and 18% less time to looking



Thylacine (*Thylacinus cynocephalus*).
Drawing by Vladimir Smirin

than solitary tammars (Blumstein et al. 1999; Blumstein et al. in review-b). These group size effects persist in a population of tammar wallabies isolated from mammalian predators for 9,500 years.

Interestingly, group size effects in some species seem to reflect a cost of aggregation; individuals seemingly forage more and look less because of increased intraspecific foraging competition. For instance, the patterns of foraging and vigilance displayed by yellow-footed rock-wallabies (*Petrogale xanthopus*) (Blumstein et al. in review-c) and quokkas (Blumstein et al. in review-d) suggest that they are also concerned about competitors, and that they forage more because they perceive additional group members as costly, not beneficial. Nonetheless, the per capita risk of predation is often reduced in larger groups and group members inevitably obtain some benefit from aggregation.

Those species with net beneficial group size effects might survive better when introduced socially than when introduced alone. Because even the most social kangaroos live in open-membership societies, and the reputedly less social wallabies (but see Blumstein et al. in review-a) are found in smaller open-membership groups, conservationists have not considered social behavior to be important when planning their reintroductions. In fact, some agencies intentionally "space" individuals when reintroducing them. We plan to test the hypothesis that social translocations can increase survival with an experiment whereby some wallabies will be reintroduced socially while others will be resettled alone. For now, it remains a reasonable (and testable) strategy that may be useful in Australia and elsewhere.

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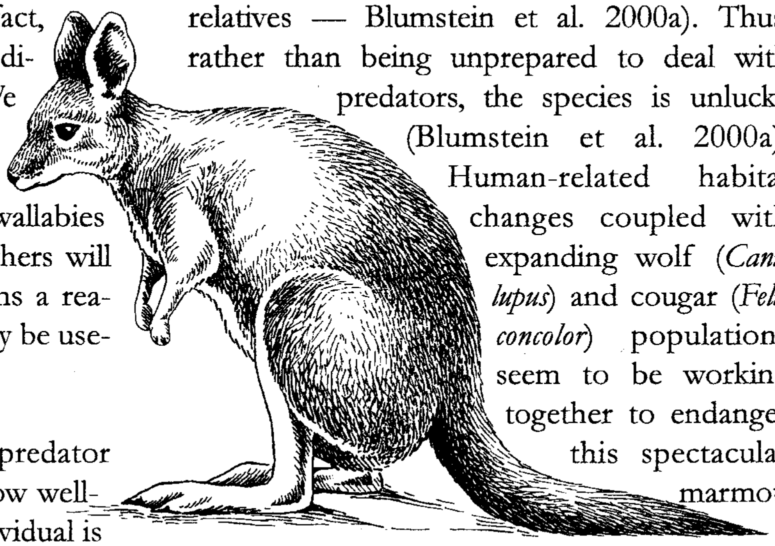
Understanding patterns of antipredator vigilance can also be used to study how well-prepared a species, population, or individual is before being translocated or introduced. Phylogenetic methods are typically used by conservation biologists to define evolutionarily significant units (e. g., Moritz 1995; Crandall et al. 2000), but comparisons between populations or species may also allow us to evaluate antipredator abilities.

Before I began studying kangaroos and wallabies, I spent over a decade studying marmots — large ground-dwelling rodents found throughout the steppes and mountains of the Northern Hemisphere (e. g., Blumstein and Armitage 1999). The Vancouver Island marmot (*Marmota vancouverensis*) is one of the world's most endangered mammals (Bryant 1999). Predation — in this case by natural predators — is implicated in its demise (Bryant 1999), and it was important to find out if this had anything to do with its inadequate antipredator behavior. Detailed comparisons with some of the 13 other species of marmots revealed that Vancouver Island marmots were no more or less prepared to deal with predators than their congeners. Vancouver Island marmots dug numerous escape burrows in their average-sized home ranges, they were as vigilant as other studied species, and, compared with their congeners, they produced the largest number of distinct alarm calls (5 different call types versus the 1–2 found in most of the other marmots, and 4 found in close relatives — Blumstein et al. 2000a). Thus, rather than being unprepared to deal with predators, the species is unlucky (Blumstein et al. 2000a). Human-related habitat changes coupled with expanding wolf (*Canis lupus*) and cougar (*Felis concolor*) populations seem to be working together to endanger this spectacular marmot.



Tammar wallaby.

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By providing examples of how an understanding of general principles of antipredator behavior may be used by conservation biologists planning reintroductions or translocations, I do not mean to imply that other behaviors are unimportant. In fact, conservation biologists should understand general principles of anything that influences reproduction or survival because it might lead to novel management strategies. Hopefully, such behaviorally-informed conservation will help control the extinction spasm that plagues Australia and the rest of the world. With luck, the sounds of the Australian night can be recovered.

Acknowledgments

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NEWS & NOTES

THE RAREST MARMOT SPECIES IS CONTINUING TO DECLINE IN THE WILD

The latest field counts of the Vancouver Island marmot (*Marmota vancouverensis*), taken in the summer of 2000, resulted in a total of 41 animals, indicating its ongoing decline.

The original colonizers of this species are believed to have crossed to Vancouver Island (British Columbia, Canada) via land bridges that existed during the Illinoian glacial period some 100,000 years ago, surviving the subsequent glacial maxima on the insular nunataks and in coastal refugia. Isolated from mainland forms for 10,000 to 100,000 years, Vancouver Island marmots have developed a number of traits that distinguish them from the other marmot species found in North America, including specific alarm calls and the chocolate-brown coloration of the new pelage with the contrasting white fur of the muzzle, forehead and breast.

In response to concerns raised by local hunters and naturalists, annual population counts of Vancouver Island marmots began in 1972. The recognition of their scarcity and patchy distribution prompted the Committee on the Status of Endangered Wildlife in Canada to list the species as endangered in 1978. Since 1972, the marmots or their fresh burrows were found at 47 sites on 15 mountains. With a single exception, all the colonies confirmed as active since the beginning of regular surveys were located within 5 adjacent watersheds on south-central Vancouver Island. The exceptional area is on Mount Washington near Comox, separated from other known colonies by 100 kilometers.

Vancouver Island marmots need habitats that provide a variety of food plants, deep soil for burrowing, suitable lookout spots, and microclimatic conditions suitable for foraging, thermoregulation and successful hibernation. Typically, they live between 1,000 and 2,000 meters above sea level, in natural meadows on steep slopes that face south to east and feature rocky debris. Steep slopes are preferred because avalanches clear them of snow in spring and permit early foraging. Avalanches also inhibit tree growth, allowing food plants favored by marmots to flourish. (Preferred foods in spring include oatgrasses, sedges and woodrush. In late summer, the marmots inhabiting natural subalpine meadows switch to broad-leaved plants such as lupines and peavine.)

Not all the marmot habitats are maintained by avalanches or snow-creep, however. Mount Washington sites are dominated by scattered alpine fir and mountain hemlock interspersed with heather and blueberries.