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Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands

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Abstract

Aim Many species find themselves isolated from the predators with which they evolved. This situation commonly occurs with island biota, and is similar to moving from the dangerous inner-city to the suburbs. Economic thinking tells us that we should expect costly antipredator behaviour to be lost if it is no longer beneficial. The loss of antipredator behaviour has important consequences for those seeking to translocate or reintroduce individuals from predator-free islands back to the predator-rich mainland, but we have neither a detailed understanding of the mechanisms of loss nor information on the time course of relaxed selection. Some antipredator behaviours are experience-dependent: experience with predators is required for their proper performance. In these cases, antipredator behaviour is lost after only a single generation of isolation, but it should be able to be regained following exposure to predators. Other behaviours may be more 'hard-wired'. The evolutionary loss of antipredator behaviour may occur over as few as several generations, but behaviours may also persist for many thousands of years of predator-free living.

Location Australia and New Zealand.

Methods I discuss the results of a series of studies designed to document the mechanisms and time course of relaxed selection for antipredator behaviour in macropodid marsupials. Controlled studies of visual, acoustic and olfactory predator recognition, as well as field studies of antipredator vigilance focused on several species of kangaroos and wallabies.

Results Visual predator recognition may be retained following 9500 years of relaxed selection, but olfactory and acoustic predator recognition may have to be learned. Insular populations allow humans to approach closer before fleeing than mainland animals. Insular species may retain 'group size effects' – the ability to seek safety in numbers – when they are exposed to any predators.

Main conclusions I suggest that the presence of any predators may be an important factor in maintaining functional antipredator behaviour. Managers should pay particular attention as to the source and evolutionary history of their population when planning translocations or reintroductions.

Keywords
Antipredator behaviour, conservation behaviour, evolutionary persistence, relaxed selection, tammar wallaby.

INTRODUCTION

Islands by their very nature are isolated, and animals on islands may experience only a subset of the selective pressures they evolved with. This is particularly true when one considers insular species and their predators. Classic biogeographical theory predicts fewer species at equilibrium on an island compared with the adjacent mainland (MacArthur & Wilson, 1967). This effect should be most pronounced when considering higher-trophic level species such as predators. Thus, species found on islands may be exposed to fewer types of predators than species found on the mainland.

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Prey have evolved a remarkable number of flexible morphological (Endler, 1988), behavioural (Seghers, 1974; Magurran *et al.*, 1995), and life-history strategies (Reznick & Endler, 1982) to avoid falling prey to predators and to guarantee leaving descendants. But these adaptations to reduce predation risk often are costly in terms of energy allocated to producing morphological defences (Parejko, 1991), rather than offspring; time allocated to wariness, rather than foraging (Hunter & Skinner, 1998); and attention (Dukas & Kamil, 2000) that must be focused on predators, rather than important activities such as mate choice (Forsgren, 1992). We should therefore generally expect that the removal of predators will lead to a loss of morphological defences and antipredator behaviour, and that life-history strategies also will shift towards a strategy that involves more parental-investment (Magurran *et al.*, 1995; Magurran, 1999).

In this review I will focus on how antipredator behaviour changes when species find themselves isolated from the predators with which they evolved. This process may happen on islands (Kavaliers, 1990), but it also happens with captive animals (Miller *et al.*, 1990; Beck *et al.*, 1994). In both cases, individuals often find themselves suddenly in suburbia – where the grass is green and the hazards of inner-city life are relaxed. How long does it take for a population to 'relax'? Is this process easily reversible? Do all types of antipredator behaviour respond similarly to the removal of some or all predators? One message from this review will be that the behavioural mechanisms underlying the loss of antipredator behaviour have important implications for the fate of individuals suddenly coming back into contact with predators, and that these behavioural mechanisms also have important implications for population management and conservation (see also Berger, 1998, 1999; Berger *et al.*, 2001).

Mechanisms of predator recognition

Antipredator behaviour – like all other traits – results from an interaction of genetic predispositions and ontogenetic experience (Curio, 1993). However, because antipredator behaviour must often be functional the first time an individual encounters a predator, most people might initially suppose that it is reasonably 'hard-wired'. (Note: by hard-wired I do not mean to imply that there is no role for experience to perfect antipredator behaviour; rather, that animals are able to perform antipredator behaviour more-or-less correctly upon their first exposure to a predator.) It may therefore seem odd that for a diversity of taxa, individuals require experience to properly perform antipredator behaviour (Griffin *et al.*, 2000). Yet, not all antipredator behaviour depends upon experience with predators or with conspecifics exhibiting proper behaviour (Owings & Coss, 1977; Curio *et al.*, 1983; Curio, 1993), and some behaviours persist for thousands of years after isolation from predators (Curio, 1966; Byers, 1997; Coss, 1999). For instance, predator-naïve California ground squirrels (*Spermophilus beecheyi*, Richardson) respond appropriately to venomous rattlesnakes, and populations retain this ability for up to 300,000 years after they have been isolated (reviewed in Coss, 1999).

Identifying the degree to which antipredator behaviour depends upon experience is crucial if one is to understand how individuals respond to the loss of their predators. If experience with predators is important for the proper performance of antipredator behaviour, then isolation for even a single generation will have a significant effect on its performance. However, if antipredator behaviour can be performed properly without experience, then these hard-wired behaviours will persist as long as it takes to have an evolutionary response to the loss of predators. All other things being equal, the most costly behaviours (i.e. those that directly reduce fitness) will be lost first, and the least costly ones may persist for many generations. There is no reason to believe that the same mechanisms or developmental trajectories (i.e. experience-dependent vs. hard-wired) underlie the suite of antipredator behaviours that a given species may employ. The mechanisms underlying antipredator behaviour are also involved in what happens when formerly isolated individuals come into contact with predators. Hard-wired behaviour may not be present, whereas experience-dependent behaviour may quickly be regained.

Antipredator behaviour of tammar wallabies

Tammar wallabies (*Macropus eugenii*, Desmarest) are a cat-sized, moderately social, macropodid marsupial. Congeners include the better known and larger grey kangaroos (*M. fuliginosis*, Desmarest, and *M. giganticus*, Shaw), and red kangaroos (*M. rufus*, Desmarest). Unlike the more social (Jarman, 1991) kangaroos who rest together, tammars spend their days mostly alone in dense cover but come out and aggregate in open grasslands to forage after sunset (Kinloch, 1973; Inns, 1980). Like their larger relatives, tammars live in open-membership societies where males associate with oestrous females and mothers and daughters may associate facultatively (Jarman, 1991; Jarman & Kruuk, 1996).

Tammars, like other Australian native animals, evolved with a variety of mammalian predators that included thylacinids – marsupial lions/tigers and dasyurids – quolls, tiger cats and devils (Archer, 1981; Robertshaw & Harden, 1989), as well as raptors and large lizards. The dingo (*Canis lupus dingo*, Linnaeus) reached Australia about 3500 years ago (Corbett, 1995) and may have been responsible for the extinction of mainland thylacines, *Thylacinus cynocephalus*, Harris (Low, 1999). Foxes (*Vulpes vulpes*, Linnaeus) were introduced in the mid-nineteenth century and quickly spread through the southern half of Australia (Coman, 1995). Cats (*Felis catus*, Linnaeus) appear to have come with Europeans (Low, 1999), after which they rapidly spread across all of Australia (Newsome, 1995).

Predation by foxes and cats is often implicated as one of a suite of factors responsible for the decline of Australian native mammals (Johnson *et al.*, 1989; Flannery, 1994), and the removal of introduced predators is often sufficient to 'recover' formerly threatened populations (Morris *et al.*, 1998; Low, 1999). It follows that a fundamental understanding of the antipredator abilities of native mammals, and specifically understanding how species respond to the loss of their predators, should be useful for ongoing conservation and management.

Tammars formerly had a discontinuous range that included south-western Australia and the peninsulas of South Australia. Their mainland range, like that of many Australian mammals, is now drastically reduced, and the genetically distinctive mainland South Australian subpopulation is extinct. However, because of the combination of Pleistocene sea-level changes and the fortuitous nineteenth century European habit of translocating animals (Low, 1999), tammars survive on a number of offshore islands (Maxwell *et al.*, 1996), and the mainland South Australian subpopulation lives in New Zealand where it is considered a non-native pest (Warburton & Sadleir, 1990; Taylor & Cooper, 1999). The mix of surviving island and mainland populations makes tammars an ideal experimental system for asking questions about how the loss of predators affects antipredator behaviour. Colleagues and I have studied the antipredator behaviour of tammars from four locations (Fig. 1) with different histories of exposure to predators.

1. Garden Island, Western Australia (32°09′S, 115°40′E) has had no mammalian predators as the island was isolated from the mainland – *c.* 7000 years ago during the last ice age (Main, 1961). There are, however, carpet pythons (*Morelia spilota*, Lacépède) which may ambush tammars, and migrating or transient eagles (*Haliaeetus leucogaster*, Gmelin, *Hieraaetus morphnoides*, Gould, *Aquila audax*, Latham) reported on the island (Brooker *et al.*, 1992) may also take the occasional animal.
2. Tutanning Nature Reserve on the Western Australian mainland (32°32′S, 117°19′E) has continuously had mammalian, avian and reptilian predators. Native marsupial predators were replaced first with dingoes and later with cats and foxes. The tammar population survived the introduction of foxes, and has recently 'recovered' following an extensive fox-baiting programme (Morris *et al.*, 1998).
3. Kangaroo Island, South Australia (35°52′S, 136°53′E) has had no mammalian predators as the island was isolated from the mainland about 9500 years ago (Lampert, 1979). There are, however, resident wedge-tailed eagles which may prey on tammar-sized animals. Europeans brought both cats and dogs to the island in the mid-nineteenth century (Waite & Jones, 1927; Inns *et al.*, 1979), but these species are largely restricted to areas around human settlements. There are no reptiles on Kangaroo Island capable of hunting adult wallabies. We studied tammars on the western part of the island in Flinders Chase National Park (Blumstein & Daniel, 2002) where dogs and cats, if present, are extremely uncommon (personal observations).
4. New Zealand tammars living around Rotorua (38°20′S, 176°25′E), where they were introduced around 1917 from Kawau Island (Warburton & Sadleir, 1990), have had no significant predators as they were translocated from the Australian mainland about 130 years ago (Warburton & Sadleir, 1990; Taylor & Cooper, 1999), where they had evolved with the full complement of native marsupial predators, dingoes, and most recently, foxes and cats (Blumstein, 2000). Recently, however, tammars around Rotorua have been poisoned and shot by humans to reduce population size.

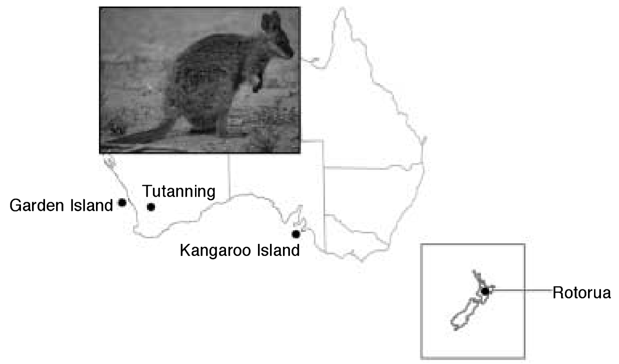

Figure 1 Sites where tammar wallaby antipredator behaviour was studied in Australia and New Zealand.

Predator recognition

Many species must first identify their predators in order to engage in appropriate antipredator behaviour (Lima & Dill, 1990). Predator recognition may involve any or all sensory modalities (i.e. visual, acoustic or olfactory). Here I will review two studies of visual and acoustic predator recognition conducted in captivity with animals from Kangaroo Island (Blumstein *et al.*, 2000) and Kawau Island (Blumstein, Daniel & Springett, unpublished data), and a captive study of olfactory predator recognition in tammars and another relative – the red-necked pademelon (*Thylogale thetis*, Lesson).

Visual and acoustic predator recognition

Briefly, tammars were isolated in holding pens and given several days to habituate to their new surroundings. Pens doubled as a testing apparatus that allowed us to expose subjects to a visual or acoustic stimulus in a controlled fashion (see Griffin *et al.*, 2001 for a schematic). Tammars were trained to forage at a location equidistant from two windows through which visual stimuli might appear. On successive mornings, tammars were baited to the central location and exposed (in a random order) to models (see Blumstein *et al.*, 2000 for images of stimuli) or to taxidermic mounts of predators (a cat, fox or thylacine), or control stimuli (a tammar, the cart all stimuli were presented on, or a blank 'treatment'). On successive afternoons, tammars were baited to the central location and were then exposed in random order to the sounds of predators (dingoes, wedge-tailed eagles), predator-related sounds (foot-thumps), or control stimuli (the call of an Australian magpie, or a blank 'treatment' – spectrograms of stimuli in Blumstein *et al.*, 2000). Responses to the presentation of all stimuli were videorecorded. The time allocated to foraging, heightened vigilance and locomotion was later calculated and compared with a baseline period prior to stimulus presentation.

We found that Kangaroo Island tammars responded to the sight of a fox and a cat by increasing their vigilance, reducing their foraging and by producing an alarm signal – foot-thumps (Blumstein *et al.*, 2000). Kawau Island animals responded to the thylacine by foot-thumping, increasing their locomotion and suppressing foraging (Blumstein, Daniel & Springett, unpublished data). Together the results suggest that visual predator recognition abilities are relatively hard-wired and apparently have been modified by different histories of relaxed selection. While Kangaroo Island tammars had presumably never seen foxes and cats in the wild, they did have to avoid predation by wedge-tailed eagles. Antipredator behaviour may persist under relaxed or modified selection because the presence of even a single predator may be sufficient to maintain functionally linked behaviours (Coss, 1999). In the case of tammars, visual predator recognition seems to rely on responding either to features shared among predators (foxes, cats and marsupial predators all have frontally placed eyes, pointy ears for detecting cryptic prey and a similar shape; Blumstein *et al.*, 2000). The loss of all predators on Kawau Island seems to have left tammars with only a crude template that equates size with risk (the model thylacine was the largest of all stimuli; Blumstein, Daniel & Springett, unpublished data).

In contrast to the sights of predators, there was no evidence that tammar acoustic predator recognition was hard-wired. Neither the Kangaroo Island nor the Kawau Island tammars responded to the predator stimuli. Kangaroo Island animals responded to the sound of foot-thumps while Kawau animals did not. This might reflect housing conditions: Kangaroo Island animals were either captive bred or had lived for >2 years in captivity before being tested. In captivity they routinely heard other individuals foot-thumping (mostly in response to keepers entering cages or nearby cages). The Kawau animals were wild-caught just prior to the experiments and lived in relatively low densities where hearing foot-thumps may have been uncommon. Thus, experience seems relatively less important for visual predator recognition than for acoustic predator recognition. Given the convergence in the visual appearance of predators but no convergence in their acoustic signals, it makes sense for species to have to learn the sounds of their predators (Blumstein *et al.*, 2000).

Olfactory predator recognition

A series of studies of predator-naïve tammars and red-necked pademelons suggest that for marsupials, olfactory predator recognition must be learned (Blumstein *et al.*, 2002). We presented individuals of both species a simultaneous choice to forage at either a feeder with a predator smell (faeces or urine) beneath it or a feeder with an herbivore smell (faeces or urine) beneath it. Predator-naïve individuals consistently failed to avoid the feeders associated with the predator smell. In contrast, the results of other studies of predator-experienced marsupials (e.g. Montague *et al.*, 1990; Gresser, 1996; Morgan & Woolhouse, 1997) suggest that they are responsive to the smells of predators and modify their foraging and space-use patterns to avoid them. Our results were initially surprising because different species of carnivores produce similar sulphurous metabolites from meat digestion (Nolte *et al.*, 1994), suggesting that prey might be selected to recognize these convergent features. Thus, we initially expected olfactory predator recognition to be relatively hard-wired.

However, considering the cost of a response may shed light on this apparent behavioural plasticity. Olfactory signals, by their very nature, are indirect cues of predation risk (Bouskila & Blumstein, 1992). Thus, animals respond to them by avoiding areas where they smell predators or by being more vigilant in those areas. Both of these responses are costly in terms of lost opportunities. Individuals with a hard-wired aversion to sulphurous stimuli might ultimately have lower fitness than those who could quickly learn to avoid the smells of predators if and only if predators were present.

Managing predation risk

Identifying predators is important, but there are a number of strategies that animals can adopt to reduce predation risk even if they are unable to identify predators quickly (Lima & Dill, 1990). Here I will discuss the effects of isolation on wariness and on whether or not animals perceive safety in numbers.

Flight initiation distance

A common antipredator behaviour is fleeing from threats (Edmunds, 1974), and a comparative metric of overall 'fearfulness' is the distance from which individuals begin to flee (Curio *et al.*, 1983; Burger & Gochfeld, 1990, 1991). We quantified 'flight initiation distance' (Bonenfant & Kramer, 1996) by noting the distance that an individual tammar began moving away from a human (e.g. Burger & Gochfeld, 1990, 1991; Bonenfant & Kramer, 1996) approaching them at a constant pace (*c.* 0.5 m s^{-1}). Insular tammars allowed a person to get significantly closer to them than mainland Tutanning animals, suggesting that current exposure to terrestrial mammalian predators makes animals wary (Fig. 2). The variation in the response demonstrates that this is a flexible antipredator behaviour. Interestingly, although not significant, New Zealand tammars ranked third in flight initiation distance, suggesting that there may be some evolutionary persistence from their relatively recent exposure to mammalian predators.

Group size effects

All else being equal, an individual in a group often has a reduced risk of predation compared with a solitary individual (Vine, 1971; Pulliam, 1973). Many species modify their time allocation in ways that suggest they perceive an

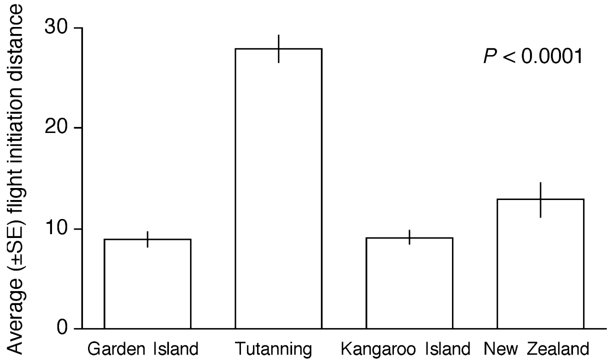

Figure 2 Flight initiation distance varied by site with tammars on the mainland fleeing at significantly greater distances than insular animals.

antipredator benefit from aggregation (Roberts, 1996; Bednekoff & Lima, 1998). Specifically, animals receiving an antipredator benefit from aggregating should have a logarithmic relationship between group size and the time allocated to vigilance (Blumstein *et al.*, 2001). By video-recording foraging tammars and counting the number of conspecifics within 10 m (the distance that tammars appear to use when defining group mates – Blumstein & Daniel, 2002), we quantified group size effects. We found that group size effects are relatively hard-wired in tammars and are found in all populations except New Zealand (Blumstein & Daniel, unpublished data). The lack of a group size effect in New Zealand may be an artefact of relatively low densities of tammars remaining where we studied them in Rotorua, or it may reflect their rapid loss following a complete relaxation of predation pressure. Like visual predator recognition, beneficial group size effects may be maintained as long as a species encounters some predators. This latter conclusion is supported by the presence of group size effects in western grey kangaroos at Tutanning and their complete loss on Kangaroo Island where adult kangaroos have much less to fear from wedge-tailed eagles than do tammars (Blumstein & Daniel, 2002).

CONCLUSIONS

Experience-dependent behaviours change rapidly following isolation from predators, whereas more hard-wired behaviours may persist for many generations. Behaviours such as flight initiation distance are very flexible; insular animals were less wary than those on the mainland, suggesting flight initiation distance is modified by experience with predators. Current evidence also suggests that olfactory and acoustic predator recognition were similarly dependent upon experience for their proper performance.

But not all antipredator behaviour is so flexible. Group size effects are retained in tammars living with any predators suggesting some sort of evolutionary constraint on the loss of group size effects in tammars. It is only relatively recently that researchers have begun to focus on life in multipredator environments (Lima, 1992; Bouskila, 1995; Sih *et al.*, 1998). The tammar wallaby results suggest that it is important to consider the entire suite of predators. The loss of all predators has different effects on more hard-wired behaviours than the loss of only some predators (Blumstein & Daniel, unpublished data).

Generally, I believe those behaviours that are likely to be particularly reliant on experience are those that have immediate costs and those where recognition errors are likely to be costly. Fleeing a non-existent predator has an immediate cost in terms of lost opportunity as well as any energetic costs associated with flight. Responding to a non-existent olfactory cue or to all sounds – whether or not they are produced by a predator – may be costly in terms of avoiding a productive foraging patch or allocating precious foraging time to antipredator vigilance. Because certain types of predators are convergent in their morphology, it may be relatively efficient to retain an ability to respond to those visual features (Blumstein *et al.*, 2000). However, the loss of all predators seems to 'degrade' the visual template rather quickly, resulting in only the crudest visual features having the ability to elicit a response (Blumstein, Daniel & Springett, unpublished data).

Conservation managers must understand the mechanism(s) underlying antipredator behaviour before releasing predator–naïve animals back into predator-rich areas. Most translocations and reintroductions (Kleiman, 1989) for conservation fail (Wolf *et al.*, 1996; Fischer & Lindenmayer, 2000), and predation is often implicated as a key factor responsible for failure (Beck *et al.*, 1991; Short *et al.*, 1992; Miller *et al.*, 1994). The presence of some predators may help maintain more 'hard-wired' antipredator behaviour. For experience-dependent behaviours, it seems that many species can be taught about the predators they are likely to encounter (Griffin *et al.*, 2000; Mclean *et al.*, 2000), and that the lessons they learn about one predator might be generalizable to other similar predators (Griffin *et al.*, 2001). However, training animals works by increasing the likelihood that an individual performs a pre-existing motor pattern. Populations that have experienced a complete loss of predators for many generations may have lost required 'behavioural precursors' to make training possible (Griffin *et al.*, 2000). Managers should pay particular attention to the source and evolutionary history of their population when planning translocations or reintroductions.

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BIOSKETCH

Dan Blumstein is broadly interested in the interface of behavioural ecology and conservation biology. His work with macropodid marsupials focuses on asking fundamental questions about the evolution and evolutionary persistence of antipredator behaviour, and applying this knowledge to help increase the success of translocations for conservation.