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ScienceDirect
Hormones and Behavior 52 (2007) 653–663
Hormones and Behavior
www.elsevier.com/locate/yhbeh

Behavioral and physiological adjustments to new predators in an endemic island species, the Galápagos marine iguana

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Received 23 February 2007; revised 9 August 2007; accepted 9 August 2007
Available online 21 August 2007

Abstract

For the past 5 to 15 million years, marine iguanas (*Amblyrhynchus cristatus*), endemic to the Galápagos archipelago, experienced relaxed predation pressure and consequently show negligible anti-predator behavior. However, over the past few decades introduced feral cats and dogs started to prey on iguanas on some of the islands. We investigated experimentally whether behavioral and endocrine anti-predator responses changed in response to predator introduction. We hypothesized that flight initiation distances (FID) and corticosterone (CORT) concentrations should increase in affected populations to cope with the novel predators. Populations of marine iguanas reacted differentially to simulated predator approach depending on whether or not they were previously naturally exposed to introduced predators. FIDs were larger at sites with predation than at sites without predation. Furthermore, the occurrence of new predators was associated with increased stress-induced CORT levels in marine iguanas. In addition, age was a strong predictor of variation in FID and CORT levels. Juveniles, which are generally more threatened by predators compared to adults, showed larger FIDs and higher CORT baseline levels as well as higher stress-induced levels than adults. The results demonstrate that this naive island species shows behavioral and physiological plasticity associated with actual predation pressure, a trait that is presumably adaptive. However, the adjustments in FID are not sufficient to cope with the novel predators. We suggest that low behavioral plasticity in the face of introduced predators may drive many island species to extinction.

Keywords: Anti-predator response; Corticosterone; Flight initiation distance; Introduced predator; Iguana; Island

Introduction

Animals on isolated islands with few or no predators typically show little escape response towards potential predators in comparison with animals on the mainland. The Galápagos islands are a famous example of an isolated archipelago featuring tame island endemics (Darwin, 1839; Curio, 1966; Stone et al., 1994). Low or practically non-existent wariness presumably results from relaxed selection during evolutionary history because of isolation from predators (Maloney and McLean, 1995; Blumstein et al., 2000; Beauchamp, 2004). However, some island species that are tame towards humans (or other potential predators) may still experience some predation during their lives, but usually from a reduced set of predators, i.e., not the fierce multitude of predators that their continental relatives experience. The lack of fear towards humans despite some ongoing predation presents an interesting counter-point towards Blumstein's (2006) multi-predator hypothesis, which we will evaluate here. This hypothesis explains the evolutionary persistence of some anti-predator behavior after the loss of some, but not all, of a species' predators. If some or even one species of predators remain, the multi-predator hypothesis predicts that prey will keep their wariness high. Only in cases where all predators are absent for a long period of time does the multi-predator hypothesis predict that prey will be unable to react to newly introduced predators. In that case, the introduction of novel predators is likely to have severe consequences for naive island species (Stone et al., 1994; Berger et al., 2001; Gittleman and Gompper, 2001).

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0018-506X/$ - see front matter © 2007 Elsevier Inc. All rights reserved.
doi:10.1016/j.yhbeh.2007.08.004

In contrast to island species with relaxed predation, species on the mainland initiate efficient escape maneuvers when faced with predator attacks and can quickly alter their behavior in response to increased predation risk by sympatric as well as newly emerging predator species (Lima and Dill, 1990; Maloney and McLean, 1995). In other words, mainland species behaviorally adjust to varying vulnerability to predation. For example, the decision to flee can be influenced by numerous factors and depends on the amount of risk animals perceive in a given circumstance (Stankowich and Blumstein, 2005). In some species, juveniles and females escape quicker than adults and males, possibly due to their smaller body size (Shine et al., 2000; Whiting et al., 2003). Furthermore, many ectotherms escape earlier when slowed by low body temperature compared to warm individuals (Rand, 1964; Smith, 1997; Cooper and Vitt, 2002).

However, it remains controversial whether and how quickly island species can develop the ability to perceive introduced species, such as dogs and cats, as life-threatening predators. For example, a comparison between the responses of experienced (mainland) and naive (predator-free island) New Zealand robins (*Petroica australis*) to an introduced mammal, the stoat (*Mustela erminea*), demonstrated that mainland robins responded strongly to the stoat, whereas island robins showed only a weak response (Maloney and McLean, 1995). Similarly, Arctic ground squirrels (*Spermophilus parryii*), isolated from snakes for 3–5 million years, have lost the ability for snake-recognition (Coss, 1999), while California ground squirrels (*Spermophilus beecheyi*), which have been isolated from snakes for 70,000–300,000 years, still recognize snakes as potential predators and respond to them appropriately (Coss, 1999).

Whether a species quickly loses anti-predator behaviour following relaxed selection depends in part on the degree to which behavior is experience dependent (i.e. learned or innate) and, ultimately, on the additional costs incurred by the respective behaviour (Blumstein and Daniel, 2002). Experience-dependent behaviour may already be lost after the first generation of isolation from predators. In contrast, more hard-wired anti-predator behaviour may persist for tens to hundreds of thousands of years following isolation (Coss, 1999). Furthermore, costly behaviour may change rapidly in response to relaxed selection by predation. As an example, fleeing from a non-existent predator has immediate costs in terms of lost opportunities for foraging, territory defense or reproduction as well as energetic costs associated with flight (Blumstein, 2002; Blumstein and Daniel, 2005).

On islands without predators, the lack of predator-recognition in native island species has become a conservation issue. Novel predators have been introduced to many previously predator-free islands either accidentally or intentionally by humans and have driven or are driving many of the island endemics to (near) extinction (Iverson, 1978; Kruuk and Snell, 1981; Atkinson, 1989). Therefore, an understanding of the degree to which anti-predator behaviour depends on experience and of the time course of predator loss is important to be able to predict how a population will respond to future predator contact (Blumstein et al., 2004; Blumstein, 2006).

Responses to a perceived threat are not restricted to the behavioral domain but also involve, and are mediated by, concomitant physiological changes (Selye, 1950; Blanchard et al., 1998; Silverin, 1998; Canoine et al., 2002). The very first flight response of a vertebrate is probably linked to epinephrine release, but due to the rapid secretion of this neurotransmitter, very few studies have addressed this mechanism in wild animals. Instead, the most commonly measured physiological indicator of responses to threats and to other environmental and social stressors are circulating plasma glucocorticoid concentrations in the blood (Moore and Thompson, 1990; Wingfield et al., 1998; Sapolsky et al., 2000; Wingfield, 2000). Although glucocorticoids are not directly involved in the initial flight response, higher concentrations of these adrenal stress hormones can help to prepare an organism to better cope with an increased probability of predatory attacks (Sapolsky et al., 2000; Romero, 2002).

In this study we investigated (1) the reaction norms of behavioral and physiological anti-predator responses in a naive island species; (2) whether naive species react to the introduction of new predators; and (3) whether behavioral changes are accompanied with changes in plasma glucocorticoid concentrations. In addition, we tested (4) the influence of age and sex on anti-predator behavior and adrenocortical responsiveness because we assumed a higher vulnerability to predation by individuals of smaller body size, in particular young animals and females (Cooper and Vitt, 1985; Díaz-Uriarte, 1999).

We chose the marine iguana (*Amblyrhynchus cristatus*) as our study species. Marine iguanas are endemic to the Galápagos islands and have been isolated from the mainland for about 5–15 million years (Rassmann, 1997). The Galápagos archipelago is of volcanic origin, and because it has never been in contact with the mainland, marine iguanas evolved without predation risk by large terrestrial animal species. Marine iguanas live in huge aggregations on the rocky shores of most islands in the Galápagos archipelago. During the day, they sunbathe on lava rocks to heat up before foraging in the cold sub- and intertidal zones (Buttemer and Dawson, 1993). The development of extensive basking behavior of marine iguanas may have been facilitated by the absence of terrestrial predators.

Starting in the last century, some of the Galápagos islands have faced a rapidly developing human population (estimated annual growth rate 6–7%) that currently has reached an estimated 30,000 inhabitants. With the people, novel predators such as domestic dogs and cats have been introduced to the islands. The growing numbers of those new predators are increasingly becoming a serious threat for most native species, including marine iguanas (Kruuk and Snell, 1981; Cayot et al., 1994; Wikelski and Nelson, 2004). A predator-related mortality rate up to 27% has been reported in some marine iguana populations (Kruuk and Snell, 1981). Because introduced predators have not reached all of the islands and gene flow between marine iguana populations of distinct islands should be low due to isolation (Rassmann, 1997), the Galápagos islands offer an interesting setting for a comparative approach where some marine iguana populations still live on islands without dogs or cats and others have become exposed to novel predators in recent times.