

ISLAND TAMENESS: REDUCED ESCAPE RESPONSES AND MORPHOLOGICAL AND PHYSIOLOGICAL ANTIPREDATORY ADAPTATIONS RELATED TO ESCAPE IN LIZARDS

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Abstract. Observers of wildlife on oceanic islands where natural predators and human beings have been scarce or absent for long intervals often have reported that wariness is greatly reduced or absent. Although this phenomenon is widely accepted and is undoubtedly real in some cases, it has rarely been the subject of scientific investigation quantitatively comparing differences in escape behavior between populations exposed to differing longterm levels of predation risk. Here we review evidence regarding effects of island occupation and predation risk on several aspects of escape behavior, refuge use, and other aspects of antipredatory defense, with emphasis on lizards. Limited data on mammals suggest that flight initiation distance and vigilance may decrease on isolated islands where predation pressure is relaxed. Bird studies indicate that on islands with low predation pressure flocking may be reduced and morphological changes leading to flightlessness have evolved frequently, limiting escape

ability. More data are available for lizards than any other taxon. In several lizard clades, flight initiation distance and other aspects of escape and refuge use have decreased on islands having low predation pressure. In some lizards restoration of predation pressure has been shown to bring about rapid increases in wariness and changes in habitat selection and morphology that facilitate escape. In Balearic lizards exposure to relaxed predation is associated with decline in the ease of tail autotomy and distance and intensity of tail movements. Because most of such studies have made one or a few island-mainland comparisons or comparisons between populations on pairs of islands, sample sizes are too small to assess significance comparatively in most studies. Metanalyses involving independent comparisons across studies show that findings among studies are consistent and significant reduction of antipredatory defense in association with reduction of predation pressure.

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The findings indicate that that reduction or loss of escape behaviors and related physiological and morphological aspects of defense is a widespread response to relaxation of predation on isolated islands. Absence of predation pressure may be predicted to affect many other antipredatory defenses, including vigilance, crypsis, aposematism, mimicry, death-feigning, pursuit-deterrent signalling, spines, body armor, weapons used primarily for defense, and others.

Key words. Autotomy, Escape behavior, Flight initiation distance, Island evolution, Island tameness, Refuge use, Predation pressure, Lizards

Resumen. Los observadores de la vida salvaje en islas oceánicas, donde los depredadores naturales y la presencia humana han sido escasos o inexistentes durante largos períodos de tiempo, frecuentemente han registrado que la cautela antidepredadora está notablemente reducida o ha desaparecido. Si bien este fenómeno es ampliamente aceptado e indudablemente real en algunos casos, ha sido raramente el objeto de una investigación científica en la cual se compararan cuantitativamente las diferencias en el comportamiento de huida entre poblaciones expuestas, a largo plazo, a diferentes niveles de riesgo de depredación. Revisamos aquí la evidencia respecto a los efectos de la ocupación de la isla y el riesgo de depredación sobre diversos aspectos del comportamiento de huida, el uso de los refugios, y otros aspectos de la defensa antidepredadora, con especial énfasis en los lagartos. Los limitados datos dis-

ponibles en mamíferos sugieren que la distancia de iniciación de la huida y la vigilancia pueden decrecer en islas aisladas donde la presión de depredación está relajada. Los estudios con aves indican que en islas con baja presión de depredación, la conducta de agrupamiento puede estar reducida y los cambios morfológicos que conducen a la pérdida de la capacidad para volar han evolucionado frecuentemente, limitando la habilidad para la huida. Hay más datos disponibles para los lagartos que para cualquier otro taxon. En numerosos clados de lagartos, la distancia de iniciación de la huida y otros aspectos de la conducta de escape y uso de los refugios han decrecido en islas con una baja presión de depredación. En algunos lagartos, la restauración de la presión de depredación se ha demostrado que va unida a un rápido incremento de la cautela antidepredadora y a cambios en la selección del hábitat y la morfología que facilitan la huida. En la lagartija balear, la exposición a una presión de depredación relajada está asociada al declive de la facilidad de autotomía caudal y a la distancia e intensidad de los movimientos de la cola. Como tales estudios se han llevado a cabo en comparaciones de unas pocas islas y zonas continentales o comparando entre pares de islas, los tamaños de muestra son demasiado pequeños para establecer su significación en la mayoría de los casos. Los metanálisis que incluyen comparaciones independientes entre los estudios, demuestran que los hallazgos de tales estudios son consistentes y que existe una reducción significativa de la defensa antidepredadora en asociación con la

reducción de la presión de depredación. Tales hallazgos indican que la reducción o la pérdida de las conductas de huida y de los aspectos fisiológicos y morfológicos relacionados con la defensa antidepredadora es una respuesta a la relajación de la presión de depredación ampliamente repartida en islas remotas. Se puede predecir que la ausencia de presión de depredación afectará a muchas otras defensas antidepredadoras, incluyendo la vigilancia, la crípsis, el aposematismo, el mimetismo, la muerte fingida, las señales de disuasión de la persecución, las espinas, las armaduras o corazas protectoras, las armas empleadas principalmente para la defensa y otras.

Palabras clave. Autotomía, conducta de huida, distancia de iniciación de la huida, evolución insular, manse-dumbre insular, uso de refugios, presión de depredación, lagartos.

Resum. Els observadors de la vida salvatge a les illes oceàniques, on els depredadors naturals i la presència humana han estat escassos o inexistents durant llargs períodes de temps, freqüentment han registrat que la cautela antipredadora està notablement reduïda o ha desaparegut. Si bé aquest fenomen és àmpliament acceptat i indubtablement real en alguns casos, ha estat rarament l'objecte d'una investigació científica, en la qual es comparessin quantitativament les diferències en el comportament de fugida entre poblacions exposades, a llarg termini, a diferents nivells de risc de depredació.

Revisem aquí, l'evidència respecte als efectes de l'ocupació de la illa i el risc de depredació sobre diversos aspectes del comportament de fugida, l'ús dels refugis, i altres aspectes de la defensa antipredadora, amb especial èmfasi a les sargantanes. Les limitades dades disponibles a mamífers suggereixen que la distància d'iniciació de la fugida i la vigilància poden decreixen en illes aïllades on la pressió de depredació està relaxada. Els estudis amb aus, indiquen que a illes amb baixa pressió de depredació, la conducta d'agrupament pot estar reduïda i els canvis morfològics que condueixen a la pèrdua de la capacitat per volar han evolucionat freqüentment, limitant l'habilitat per la fugida. Hi ha més dades disponibles per als sargantanes que per qualsevol un altre taxó. A nombrosos clades de sargantanes, la distància d'iniciació de la fugida i altres aspectes de la conducta de fuga i ús dels refugis han decrescut en illes amb una baixa pressió de depredació. En alguns sargantanes, la restauració de la pressió de depredació s'ha demostrat que va unida a un ràpid increment de la cautela antipredadora i a canvis en la selecció de l'hàbitat i la morfologia que faciliten la fugida.

A la sargantana balear, l'exposició a una pressió de depredació relaxada està associada al declivi de la facilitat d'autotomia caudal i a la distància i intensitat dels moviments de la cua. Els estudis s'han dut a terme en comparacions d'unes poques illes i zones continentals o comparant entre parells d'illes, encara que les grandàries de mostra són massa petites per establir la

seva significació en la majoria dels casos. Els metanàlisis que inclouen comparacions independents entre els estudis, demostren que les troballes de tals estudis són consistents i que existeix una reducció significativa de la defensa antipredadora en associació amb la reducció de la pressió de depredació. Tals troballes indiquen que la reducció o la pèrdua de les conductes de fugida i dels aspectes fisiològics i morfològics relacionats amb la defensa antipredadora és una resposta a la relaxació de la pressió de depredació àmpliament repartida a illes remotes. Es pot predir que l'absència de pressió de depredació afectarà a moltes altres defenses antipredadores, incloent la vigilància, la crípsis, el aposematisme, el mimetisme, la mort fingida, els senyals de dissuasió de la persecució, les espines, les armadures o cuirasses protectores, les armes emprades principalment per a la defensa i altres.

Paraules clau. Autotomia, conducta de fugida, distància d'iniciació de la fugida, evolució insular, mansuetud insular, ús de refugis, pressió de depredació, sargantanes.

INTRODUCTION

Numerous observers have noted that some birds and other animals on isolated oceanic islands lacking mammalian predators allow observers to approach closely without attempting to flee (Darwin, 1839; Lack, 1947; Curio, 1966), suggesting that escape behavior decays in the absence of

predators or under reduced predation pressure. Even the morphological means of escape may be diminished or lost under island conditions of reduced predation pressure, perhaps the most famous examples being the flightless dodo, *Raphus cucullatus* (Diamond, 1982; Roberts and Solow, 2003). Such considerations have stimulated limited research on the broader problem of the relationship between antipredatory defenses and predation pressure, including studies of the effects of living on predator-free islands on vigilance and predator recognition as well as escape (Blumstein and Daniel, 2002, 2005) and a simulation study suggesting that ability to recognize predators and flee may decay most rapidly in the absence of predators when costs of escaping and mutation rates are high (Blumstein et al., 2006). The latter finding is consistent with the hypothesis that antipredatory behaviors and structures may be reduced or lost when predation risk is absent or low because these antipredatory adaptations are costly to maintain. Presumably, when risk is low, they may be reduced or lost due to drift if not costly or due to natural selection against them if costly.

Although many anecdotal reports of reduced wariness on oceanic islands, sometimes called insular (or insular) tameness, exist, few studies have quantified differences in wariness between island and mainland populations or among island populations exposed to different regimes of predation pressure. Most of these studies have focused on mammals or lizards.

Tammar wallabies (*Macropus eugenii*) from island populations in Australia and New Zealand exhibit flight initiation distances only about one third as long as those from the Australian mainland (Blumstein, 2002). These wallabies in New Zealand, which were introduced only 130 years prior to the study, have lost the effect of group size on vigilance, i.e. the decrease in vigilance as group size increases, in response to mammalian predators in their absence (Blumstein et al., 2004). Flight initiation distance by Vancouver Island marmots (*Marmota vancouverensis*) was not significantly shorter than in mainland congeners, which is consistent with the abundance of avian and mammalian predators on Vancouver Island (Blumstein et al., 2001). These mammalian studies suggest that escape behavior and vigilance may wane or be lost on islands in the absence of mammalian predators, but are likely to be retained on islands in the presence of predators.

Much research has been devoted to understanding causes of recent extinctions of birds on islands following human arrival (e.g., Olson and James, 1982; Steadman, 1995; Holdaway, 1999; Holdaway and Jacomb, 2000; Grayson, 2001). In New Zealand extinction of birds in historic times has been attributed to susceptibility of endemic species to introduced predators as a consequence of a previous loss of escape behavior by endemic birds, including loss of the ability to fly (Duncan and Blackburn, 2004). Fifteen flightless endemic species in New

Zealand have close relatives elsewhere that fly, emphasizing the frequent loss of escape ability due to morphological changes under relaxed predation pressure (Duncan and Blackburn, 2004). Another study compared flocking behavior of 46 bird species on 22 islands from several oceans where predation pressure is low with flocking by the most closely related species on the associated mainland (Beauchamp, 2004). Flocking, as indicated by mean and maximum flock sizes, diminished in birds on the isolated islands. In 35 species the island and mainland populations did not differ, but of the 11 remaining species, 10 showed reduced flocking on the islands (Beauchamp, 2004). As for birds, extinction rates of reptiles in the last 10,000 years are much higher on islands than on mainland, and have often been associated with introductions of specific predators, notably dogs, cats, rats, and mongoose (Case et al., 1992). Although information on escape behavior of the reptiles is lacking, the extinguished species very likely had ineffective escape behavior compared to related mainland species.

Autotomy, the voluntary severing of a body part by a prey as a last resort when overtaken by a predator, is a complex defense that combines morphological adaptation for breakage of expendable body parts with behavioral and physiological features that enhance the effect of autotomy on ability to escape. Although autotomy occurs in a wide range of vertebrate (reviewed by Cooper, 2007) and

invertebrate (reviewed by Fleming et al., 2007) taxa, it has been studied most thoroughly in lizards (reviewed by Arnold, 1988; Bateman and Fleming, 2009). Ability to autotomize the tail by breaks occurring in intravertebral planes where resistance to breakage is reduced appears to be the ancestral condition in lizards, but this ability has been lost in several lineages (Arnold, 1988; Zani, 1996). Autotomy does not occur in some of those lineages, but in others the ability to autotomize the tail has been evolved secondarily, but occurs at points between vertebrae (Arnold, 1988; Zani, 1996). In lacertid lizards, autotomy occurs intravertebrally (Arnold, 1996).

Autotomy may permit a lizard to escape while a predator is distracted by the tail, which may thrash violently on the ground or in a predator's mouth or talons (Clark, 1971). Nevertheless, autotomic tail loss is costly. Among the costs that directly affect escape ability are loss or reduction of ability to use autotomy again as a defense until the tail regenerates (Arnold, 1988) and decrease in running speed (Ballinger et al., 1979; Cooper et al., 2009a). Other costs of autotomy are loss of energy reserves in lipid stored in the tail, which can lead to reduced clutch size and make lizards more susceptible to starvation (Daniels, 1984), as well as impairment of foraging ability (Martín and Avery, 1997), and reduced social status, including mating opportunities (Fox and Rostker, 1982).

Predictions of effects of isolation from predators on escape behavior, running speed, and autotomy in lizards

Here we review the limited, but growing, evidence about effects of exposure to reduced pressure predation in island populations of lizards on antipredatory adaptations. To date the preponderance of evidence is limited to escape responses and refuge use. However, some evidence suggests that relaxation of predation pressure can also affect running speed and associated morphology that may strongly affect escape ability. Reduction of predation pressure may also lead to modification of several aspects of autotomy, including willingness to voluntarily autotomize tails, latency to autotomize when restrained, distance and duration of post-autotomic tail movements, and vigor of tail movements (Cooper et al., 2004).

Optimal escape theory predicts that flight initiation distance based on a prey's assessment of predation risk, benefits that may be obtained by not fleeing during a predator's approach, the prey's assessment of risk, lethality of the predator, and the prey's fitness at the outset of the encounter with the predator (Cooper and Frederick, 2007a, in press). Optimal escape theory has been extended successfully to predict the distance fled and probability of entering a refuge (Cooper, 2009a). A closely related model of refuge use predicts hiding time (time spent in refuge before emerging) from the same variables (Cooper and Frederick, 2007b). Among these variables, the perceived predation

risk is likely to differ in general between populations that have experienced very different levels of predation pressure, especially those in which predation by certain taxa of predators has been absent versus present. Perceived predator lethality also is likely to differ among populations exposed to different types of predators. The qualitative effects of perceived predation risk (risk of being overtaken) and predator lethality upon contact on escape decisions are similar: flight initiation distance, distance fled, probability of entering refuge, and

hiding time all increase as assessed risk and lethality increase (Cooper and Frederick, 2007a,b; in press; Cooper, 2009a; table 1).

Results of large numbers of studies of diverse prey exposed to numerous predation risk factors are consistent with optimal escape theory's predictions for flight initiation distance and hiding time (reviewed for flight initiation distance by Stankowich and Blumstein (2005) and by Cooper, 2009a) for hiding time). Under the assumption that prey in island populations where predators are scarce

| Character | Effects of reduced predation pressure | Effects of increased predation pressure |
|--------------------------------|---------------------------------------|---|
| Escape | | |
| Flight initiation distance | ↓ | ↑ |
| Distance fled | ↓ | ↑ |
| Refuge use | | |
| Probability of entry | ↓ | ↑ |
| Hiding time | ↓ | ↑ |
| Locomotion | | |
| Running speed | ↓ | ↑ |
| Hind limb length | ↓ | ↑ |
| Table 1 continued | | |
| Tail length | ↓ | ↑ |
| Autotomy | | |
| Ease (force needed) | ↑ | ↑ |
| Distance moved by shed tail | ↓ | ↑ |
| Thrashing rate of shed portion | ↓ | ↑ |
| Duration of movement | ↓ | ↑ |

Table 1. Predicted effects of altered predation pressure on islands on aspects of antipredatory behavior, locomotion, and autotomy

or absent perceive risk of being captured and lethality as lower than prey where predation pressure is greater, optimal escape theory provides a well-supported basis for the predictions for lizards, as well as other prey, that flight initiation distance, distance fled, probability of entering refuge and hiding time are shorter in populations exposed to reduced predation pressure, especially on islands where predators are absent or nearly so. In a large majority of studies of escape behavior and refuge use, including all of those on lizards described below, researchers have served as experimental surrogate predators. Although responses to specific types of predators might be obscured using this method (Stuart-Fox et al., 2006), results of studies using of human beings as predators have consistently conformed to predictions of optimality theory (Stankowich and Blumstein, 2005; Cooper 2008). Use of human beings as experimental predators has been highly successful and is widely accepted.

Because prey that run faster are presumably better able to outrun predators or to reach refuges before being overtaken, higher predation pressure (and faster predators) should favor faster running speed and morphological traits that make greater speed possible. In lizards, longer hind limb length is associated with greater speed both interspecifically and intraspecifically (Losos and Irschick, 1996; Vanhooydonck et al., 2006). Therefore, lizards on islands with reduced predation pressure may be

predicted to run less quickly and to have shorter hind limbs than those in populations exposed to greater predation pressure.

Because autotomy is a very costly defense that requires development and maintenance of morphological, physiological, and associated behavioral mechanisms, it may be predicted that relaxation of predation leads to reduced ability and tendency to autotomize tails and reduced ability of the shed tail as a distractor (Table 1). Lizards subjected to low predation pressure for a relatively short time might exhibit a higher threshold risk of being killed in order to induce autotomy. Evolution of morphological changes that make autotomy more difficult or impossible is likely to require longer isolation from predators, especially complete loss of intravertebral fracture planes. Physiological changes, such as reduction of the capacity for violent and/or prolonged thrashing of the tail, might require an intermediate time to evolve.

Islands, predation pressure, and lizard antipredatory defenses

Galapagos island lizards. In this 150th anniversary year of Darwin's publication of evolutionary theory, we begin with evidence from research relating escape behavior to predation pressure that has been conducted in the Galapagos Islands using lava lizards (*Microlophus*, formerly *Tropidurus*) and marine iguanas (*Amblyrhynchus cristatus*). Lizard populations have

experienced low predation rates on the islands for 5-15 million years (Berger et al., 2007; Rödl et al., 2007), long enough to have evolved island tameness should it exist. Predators such as cats and dogs have been introduced by man on some islands beginning about 150 years ago (Rödl et al., 2007), which has provided two groups of researchers opportunities to examine effects of relatively recently introduced predators on escape behavior by lizards where insular tameness is likely to have evolved.

Several species of *Microlophus* occur on various islands, where they are exposed to different predator suites, including introduced feral cats, rats, as well as snakes. Stone et al. (1994) noted that feral cats frequently kill lava lizards, and predicted that flight initiation distance and distance fled would increase in response to presence of each of the three types of predators. On islets lacking cats, mean flight initiation distance was only 0.2 – 1.1 m and distance fled 0.5-0.7 m, suggesting that tameness has evolved there. Where cats have been introduced and are major predators on lava lizards, flight initiation and distance fled are predicted to be greater on adjacent island having than lacking cats under the assumption that exposure to cats has led to increased wariness. The longest two mean flight initiation distances (1.4 and 1.6 m) occurred on islands where cats are present, and the range of mean flight initiation distance was 0.7 – 1.6 m. The three greatest values of mean distance fled were on the three islands where cats were present (0.7 – 1.3 m).

Stone et al. (1994) compared behaviors in populations on adjacent islands differing in presence/absence of predators. Using data from nine populations of lava lizards on eight islands, they found that flight initiation distance was significantly greater in populations with cats present in all three comparisons of populations between adjacent islands having and lacking cats (Figure 1). Distance fled was significantly greater on islands where cats are present in two of the same three interisland comparisons (Stone et al., 1994). In the third, nonsignificant comparison, the mean distance fled was nearly twice as great on the island where cats were present than where they were absent, but this difference was not significant due to high variability and small sample size (Stone et al., 1994). In a group of three islands where cats were absent, none of the interisland differences were significant for either flight initiation distance or distance fled

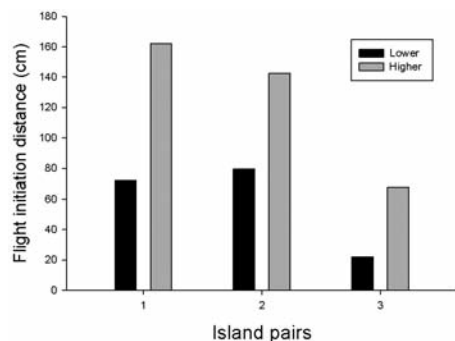


Figure 1. Mean flight initiation distances for lava lizards (*Microlophus*) on three pairs of adjacent island in the Galapagos Archipelago that differ substantially in predation pressure. Note the longer flight initiation distance for the island having higher predation pressure in each pair. Data from Stone et al. (1994)

(Stone et al., 1994). Presence of rats and snakes on islands had no consistent effect on flight initiation distance or distance fled.

Because predator-free islands served as controls for the comparisons with islands with predators present, it was tacitly assumed that any differences were due to presence of predators. As a corollary, it may be predicted that flight initiation distance and distance fled, do not differ significantly among adjacent islands lacking cats. A test of the combined predictions of difference when predation pressure differed and lack of difference when predators were absent in both island, the results matched predictions in all six interisland comparisons (three between islands having or lacking cats and three between pairs of islands lacking cats) for flight initiation distance (sign test, $P = 0.03$, 2-tailed). For distance fled, five of six comparisons were as predicted (sign test, $P = 0.11$, 1-tailed) and all six are in the predicted direction (sign test, $P = 0.03$, 2-tailed). These new tests using the findings of Stone et al. (1994) are not very robust, but provide some comparative evidence for island tameness and its reversal in the presence of an introduced predator.

The study of lava lizards provided the first quantitative evidence that (1) linked escape behavior to a specific predator of lizards and that (2) lizards on isolated oceanic islands lacking major predators had evolved island tameness. The findings support a role of predation in restoring wariness to some degree, but given the relatively

brief presence of cats, it is uncertain to what extent the increased wariness may be a consequence of experience or evolutionary change (Stone et al., 1994). However, antipredatory responses in some cases can be restored rapidly by learning during initial encounters with predators in birds (Maloney and McLean, 1995) and lizards (Rödl et al., 2007). Further comparative studies of lizards on other island chains and of close relatives in mainland settings where predation pressure is much higher and has been so for a very long time are needed to adequately assess effects of isolation from predation on escape behavior.

Marine iguanas are among the species described long ago as exhibiting reduced wariness (Darwin, 1839), and are one of few species in which island tameness is known to many nonbiologists. However, their escape behavior has only recently been studied (Berger et al., 2007; Rödl et al., 2007). Because marine iguanas are much larger than lava lizards, dogs are important predators. On islands where feral cats and dogs were introduced about 150 years ago, lizards have substantially longer flight initiation distances than on an island where dogs and cats have never been introduced (Rödl et al., 2007). Flight initiation distance was ca. 1 m where predators were absent; it was about 3 m on an island with intermediate predation pressure, and 4 m on a third island with highest predation pressure (Rödl et al., 2007; figure 2).

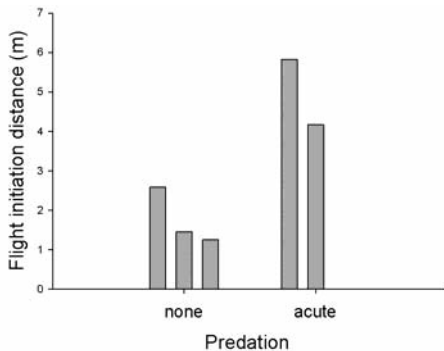


Figure 2. Flight initiation distance by marine iguanas (*Amblyrhynchus cristatus*) on five Galapagos islands having no predators or very high predation rates by introduced predators. Data from Berger et al. (2007)

Additional comparisons by the same research group showed that on islands with no introduced predators, flight initiation was longer on Santa Fe where hawks are present than on two other islands where hawks are absent (Berger et al., 2007). Flight initiation distance at three sites with infrequent predation by introduced predators did not differ consistently from that in three sites lacking introduced predators, at least in part due to differences among sites in presence of natural predators and habituation to people (Berger et al., 2007). Of greater interest, the flight initiation distance was substantially longer on two islands where predation by introduced predators, especially dogs, is frequent (4.4 – 5.8 m).

Among lizards that fled, distance fled was greater at sites with high predation pressure than at the other sites (Berger et al., 2007). Although only a small proportion of lizards hid in crevices when approached, the proportion that entered these refuges

was significantly greater at the sites having high predation pressure than at the other sites (Berger et al., 2007).

When stressed by being attacked by predators, vertebrate prey increase production and release of glucocorticosteroids, the primary one for lizards being corticosterone. In marine iguanas, this stress response was absent among naïve individuals in an island population lacking introduced predators (Rödl et al., 2007), being greater in populations exposed to introduced predators (Berger et al., 2007). However, repeated approach by the experimenters induced higher circulating corticosterone levels, suggesting that lizards with islet tameness do not initially perceive approaching experimenters as threatening. Upon repeated approach, they become warier and exhibit a stress response. Thus, the stress response appears to be intact, but is not expressed until threat is assessed.

Anolis in the Caribbean. Although escape behavior per se has not been examined in relation to predation pressure in island anoles, experimental introduction of the predatory lizard *Leiocephalus carinatus* has revealed effects of predation relevant to escape. Introduction of *L. carinatus* to several islands induced a shift of *Anolis sagrei* to higher perches (Schoener et al., 2005; Losos et al., 2006). The proportion of *A. sagrei* sighted on the ground declined from slightly less than 0.4 to less than 0.1 in one year (Schoener et al., 2005; Losos et al., 2006), presumably facilitating avoidance of and escape by climbing

out of reach of the terrestrial *L. carinatus*. Similar changes did not occur on control islands. Initially, having longer hind limbs conferred superior survival in the presence of *L. carinatus*, but after *A. sagrei* switched to elevated perches, selection for movement on narrow, irregular surfaces on tree trunks and branches favored shorter hind limbs (Losos et al., 2006). Such experimental studies provide a promising approach to studying rapid changes in escape behavior with controlled differences in predation pressure.

Gulf of California. The spiny-tailed iguana, *Ctenosaura hemilopha*, occurs on the mainland of the southern part of the Baja California, and on Cerralvo Island 11 km offshore in the Gulf of California. The only major terrestrial predator on Cerralvo Island is the domestic cat, which was introduced only during the two decades before a study, and some raptors; on the mainland there are several species of natural mammalian predators as well as cats and dogs, and raptors are more abundant (Blázquez et al., 1997). *Ctenosaura hemilopha* may have been introduced to Cerralvo Island by people (Murphy, 1983), but the origin of the population there is uncertain. Thus, as for most of the other lizard studies discussed above, it is unclear to what extent any difference in escape behavior between populations reflect evolutionary changes or differences in degree of experience with predators.

On Cerralvo Island, flight initiation distance by *C. hemilopha* is much shorter than on the mainland (Blázquez

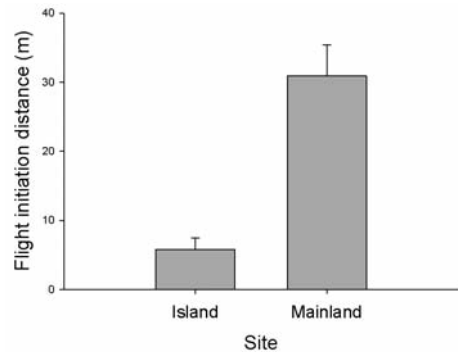


Figure 3. Flight initiation distance (mean + SE) for *Ctenosaura hemilopha* from a mainland population on Baja California and an island in the Gulf of California. Data from Blázquez et al. (2003)

et al., 1997; Figure 3). Another indication that antipredatory behavior has diminished is that lizards on the mainland stay closer to refuges (0.7 m) than do lizards on Cerralvo Island (5.1 m; Blázquez et al., 1997). Because flight initiation distance in lizards increases as distance to the nearest refuge increases, the relaxation of escape behavior on Cerralvo Island is even greater than indicated by the difference in flight initiation distance alone. Other findings that may reflect the difference in predation pressure between the populations were a greater tendency to flee as first reaction by mainland lizards versus greater tendency to watch the approaching investigator by lizards on Cerralvo Island, and occupation of perches much higher above ground by mainland lizards despite availability of high perches on the island (Blázquez et al., 1997). All evidence for *C. hemilopha* is consistent with island tameness as a consequence of lowered predation threat.

Shallenberger (1970) studied flight initiation distance in *Sauromalus obesus* from the mainland and two species, *S. varius* and *S. hispidus*, from islands in the Gulf of California. Although some of the findings appear to be correct, the experiments suffer from effects of possibly extensive pseudoreplication and lack of control for group size. *Sauromalus obesus* on the mainland and island *S. hispidus* appeared to have equal flight initiation distances. *Sauromalus varius* permitted extremely close approach when on feeding grounds, but were wary when near their refuges. Comparisons between *S. obesus* and *S. varius* on feeding grounds far from refuges could not be made because *S. obesus* stays on rocks close to refuges.

Relaxation of predation pressure might have allowed *S. varius* to use feeding grounds far from shelter. That lizards on feeding grounds permit very close approach and even handling is very likely a consequence of isolation from mammalian predators.

Podarcis in the Mediterranean Basin: oceanic and sky islands

The Iberian wall lizard, *P. hispanica*, is widely distributed on the mainland of the Iberian Peninsula; its close relative *P. atrata* (formerly *P. h. atrata*) is restricted to the Columbretes islands in the Mediterranean near the Spanish coast. A viper (*Vipera latastei*) that eats these lizards is present on the mainland, and was present in the Columbretes, but has been absent on the islands for more than 100 years (Van Damme and Castilla, 1996). Despite the relatively

brief absence of vipers, *P. atrata* exhibited reduction in some aspects of defensive responses to chemical cues from the viper (Van Damme and Castilla, 1996) even though island and mainland lizards exhibited similar tongue-flick rates, which indicates that the island lizards they continued to sample environmental chemicals, but did not respond as strongly to predator scent. In particular, *P. atrata* showed less frequent foot-shaking and tail-vibration responses, both of which are specific to antipredatory contexts, when exposed to scent from the viper, than did *P. hispanica* from a mainland population (Van Damme and Castilla, 1996).

Ten individuals of *Podarcis sicula*, the Italian wall lizard, were transferred from the Adriatic island Pod Kopište to found a new population on the nearby island Pod Mrčaru in 1971. Approximately 35 years later, lizards on the two islands exhibited differences in escape behavior and predation pressure consistent with island tameness. Flight initiation distance and distance fled, and hind limbs were longer on the island of Pod Kopište than on Pod Mrčaru (Vervust et al., 2007). Mammalian and other terrestrial predators were absent on both islands, but higher frequency of attacks on plasticine lizard models by birds on Pod Kopište than on Pod Mrčaru suggests that predation pressure is greater on Pod Kopište (Vervust et al., 2007). Thus, aspects of escape behavior and morphology important for rapid running declined rapidly where predation pressure was lower.

Podarcis lilfordi, the Balearic lizard, is endemic to the Balearic islands. It is extinct on the main island of Menorca as a consequence of predation by introduced predators, but occurs on 16 islets adjacent to Menorca (Pérez-Mellado, 1989, 1998). Predation pressure differs greatly among islets. On Aire, predation pressure is very lax: kestrels (*Falco tinnunculus*) visit at times, but do not nest there, and no other vertebrate predators occur (Pérez-Mellado, 1989). On the islets of Rei and Colom, kestrels nest, shrikes (*Lanius spp.*) visit, established populations of rats exist, and cats and dogs have been present in the recent past (Pérez-Mellado, 1989; Cooper et al., 2009b). My colleagues and I have studied aspects of escape behavior, refuge use, and tail autotomy in these lizards under the hypothesis that, due to relaxed predation pressure on Aire, the escape and refuge use would be less pronounced on Aire than on Rei and that autotomy would not be used as readily by lizards on Aire as by those on Colom (Cooper et al., 2004, 2009).

The information on escape and refuge use in *P. lilfordi* in this and the following three paragraphs is from Cooper et al. (2009b). Flight initiation distance by *P. lilfordi* on Aire was significantly shorter than that on Rei at each of three predator approach speeds tested: the greatest difference occurred at the slowest approach speed, flight initiation distance on Aire being less than half that on Rei (Cooper et al., 2009b; Figure 4 for slow approach speed). A significant interaction occurred between approach speed and

islet, but its effect size was small ($\eta^2 = 0.11$). The effect of approach speed was substantial ($\eta^2 = 0.35$), but the effect size of islet was much larger ($\eta^2 = 0.61$). Because approach speed is a major predation risk factor affecting flight initiation distance (Stankowich and Blumstein, 2005; Cooper, 2009b), the greater effect size of islet indicates a very strong difference in escape behavior between islets.

Lizards on Rei fled much longer distances than those on Aire despite their greater flight initiation distance, nearly four times as far (Figure 4). The effect size was extremely large ($\eta^2 = 0.97$), again indicating a great difference in the direction predicted by relaxation of predation pressure.

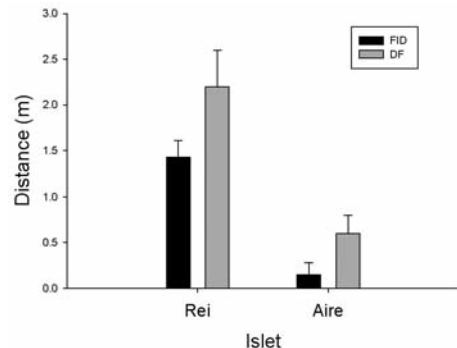


Figure 4. Flight initiation distance and distance fled (mean + SE in m) for *Podarcis lilfordi* on the Menorcan islets Rei (higher predation pressure) and Aire (lower predation pressure). Data from Cooper et al. (2009b)

On Aire slightly less than half of lizards entered refuges at the end of escape runs, but on Colom 93% of lizards entered refuges such as holes in the ground, crevices, or dense bushes. This difference was highly significant. This result strengthens the finding of a

difference in distance fled because distance fled is truncated when lizards enter refuge. Although we did not measure distance to refuge, abundant nearby refuge sites were available to lizards on both islets. For lizards that entered refuges, hiding time was far longer on Rei than on Aire, almost nine times as long, and had a large effect size ($r^2 = 0.63$). Longer hiding time is predicted by optimal refuge use theory for prey that assess risk upon emergence as being greater (Martín and Lopez, 1999; Cooper and Frederick, 2007b), which should be the case when predation pressure is elevated.

Divergence time between the Rei and Aire populations of *P. lilfordi* is 280,000 years (Brown et al., 2008), providing ample time for evolution of differences in escape behavior and refuge use. On Aire lizards have not entirely lost escape behavior. Their mean flight initiation distance of about 1.5 m at the slowest approach speed is greater than that of some mainland species (Cooper, 2006, 2009b), and nearly half of lizards entered refuges. The reduction in escape behavior by *P. lilfordi* is incomplete, and not as drastic as that seen in some prey species on remote oceanic islands where mammalian predators have been absent for millions of years. Because changes in escape behavior can occur rapidly when predation pressure is relaxed or intensifies (Stone et al., 1994; Van Damme and Castilla, 1996; Berger et al., 2007), *P. lilfordi* on Aire would seem to have had long enough to evolve more pronounced tameness had predation be

absent or rare throughout the interval of separation between the Rei and Aire populations. Infrequent predation undoubtedly continues on Aire, and very likely varies over time with the frequency of visits and nesting by raptors and other birds that eat lizards, which would account for maintenance of the diminished escape behaviors.

Several aspects of autotomy vary among populations of *P. lilfordi* on the islets Aire and Colom and a mainland population of *P. hispanica*, a closely related congener (Arnold, 1989); this variation occurs in a graded manner that corresponds to degree of predation pressure as indicated by diversity and abundance of predators present (Cooper et al., 2004). Predation is most intense on the mainland and least intense on Aire (Pérez-Mellado, 1989; Cooper et al., 2004). In two-minute trials in which lizards were held by vernier calipers pressed to the tail with sufficient force to prevent escape, *P. lilfordi* from Aire and Colom voluntarily autotomized their tails less frequently and with longer latency than mainland *P. hispanica* (Cooper et al., 2004; Figure 5). They were also more likely than lizards from the mainland to roll their bodies, which appeared to be necessary to exert sufficient force to break the tail (Cooper et al., 2004). Induction of autotomy by squeezing tails with the calipers required much greater force for lizards from Aire than in the other populations, and appeared to require intermediate force for lizards on Colom (Cooper et al., 2004).

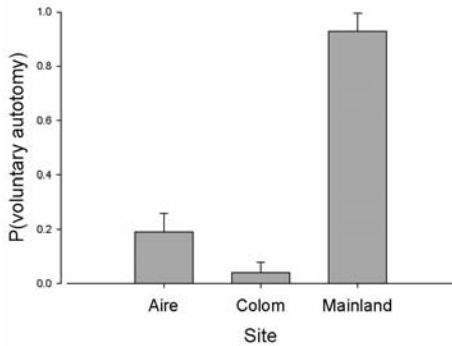


Figure 5. Probabilities that *Podarcis lilfordi* on the Menorcan islets of Aire (low predation pressure) and Colom (higher predation pressure) and *P. hispanica* on the Iberian Peninsula (still higher predation pressure) voluntarily autotomized their tails within in two minutes of being restrained by Vernier calipers. Error bars are 1.0 SE. Data from Cooper et al., 2004

Once a tail broke, the shed part for lizards from Aire thrashed with much less vigor than parts from lizards in the other populations (Cooper et al., 2004). Tails from *P. hispanica* moved farthest before stopping (Cooper et al., 2004). In *P. lilfordi* shed tail segments from Colom moved an intermediate distance and those from Aire moved the shortest distance (Cooper et al., 2004). Shed tails from Aire thrashed for a somewhat shorter time than those from Colom, but this difference was not significant (Cooper et al., 2004). However, tails from *P. hispanica* moved for much shorter times than those from the island populations of *P. lilfordi*, their stored energy presumably being depleted rapidly by the extreme vigor of movement (Cooper et al., 2004). A test of concordance among rankings of all of the autotomy variables revealed strong agreement across the three populations, indicating consistent

decline in intensity of several aspects of autotomy as predation pressure decreases (Cooper et al., 2004).

A related finding was that tails are longer relative to body length in the Colom than Aire population of *P. lilfordi* (Cooper et al., 2004). Because longer tail length is associated with greater running speed in lizards (Ballinger et al., 1979; Zhi-Hua and Xiang, 2005; Cooper et al., 2009a), this difference may reflect morphological evolution of tail length adapting populations to degree of predation pressure. On Aire, where predation pressure is low, lizards may allocate some of the energy diverted to growth and maintenance of extra tail length on Colom to other uses.

Aspects of autotomy in nine species of European lacertids, including seven of *Podarcis*, including *P. lilfordi* and *P. hispanica*, exhibited variation consistent with that found by Cooper et al. (2004; Pérez-Mellado et al., 1997). Autotomy was easier to induce and shed tails moved longer in island than mainland species (Pérez-Mellado et al., 1997). *Podarcis milensis* from the Island of Milos was exceptional in that autotomy was easy to induce and the duration of tail movements was as high as in mainland lacertids (Pérez-Mellado et al., 1997). However, these findings reinforce the importance of predation pressure because predation pressure is high on Milos (Pérez-Mellado et al., 1997). All available evidence suggests that several aspects of autotomy change in ways that reduce its utility as a defense when predation pressure is low. On the other hand tails may be broken and eaten by

conspecifics more frequently on islands where very high population densities occur, which may be a contributing factor to evolution of greater difficulty of autotomizing tails (Pérez-Mellado et al., 1997).

Areas of mountains at high elevation can be ecologically analogous to isolated islands for animals not only because populations at lower latitude and higher elevation may be isolated from conspecific populations at lower elevation and higher latitude, but also because predation pressure may be reduced at higher elevation. Three lines of evidence indicate that in northern Spain the Iberian wall lizard, *Podarcis muralis*, in a population at 308 m elevation experiences substantially higher predation pressure than a population at 1185 m (Diego-Rasilla, 2003). Frequency of broken tails indicating autotomic loss was much greater (88%) in the lower population than in higher population (33%, Diego-Rasilla, 2003). Because highly efficient predators kill prey; only prey that survive can be observed (Schoener, 1979). Therefore, this finding does not demonstrate that predation pressure is greater at the lower site. Nevertheless, such a large difference in tail break frequency is highly suggestive. More convincing is a significantly higher frequency of attacks by predators on plasticine models of lizards at the lower elevation site (56%) than at the higher site (24%, Diego-Rasilla, 2003). Direct observations revealed two species of snakes that eat lizards, raptors, and the pine marten, *Martes martes* at the lower site, but only a single raptor species at

the higher site (Diego-Rasilla, 2003). Collectively, the higher rates of tail breakage and attacks on prey models and the differences in predators provide convincing evidence that predation pressure is higher at the lower elevation site.

Flight initiation distance by *P. muralis* was more than 2 ½ times longer at the lower elevation than at higher elevation (Diego-Rasilla, 2003). The probability of entering refuge at the end of an escape run was far greater for lizards at the lower site, where all lizards hid in refuges, than at the higher site, where only 19% entered refuges (Diego-Rasilla, 2003). The difference in refuge entry was not a consequence of a difference in proximity to refuge sites because initial distance from refuge did not differ significantly between sites (Diego-Rasilla, 2003). Distances fled did not differ at the high and low elevation sites, but this finding may be misleading because distance fled was limited by distance to the refuge for a much higher proportion of lizards at the lower elevation site. The findings for *P. muralis* show that escape behavior and refuge use are relaxed in a sky island population where predation pressure is reduced, which is consistent with findings for oceanic islands.

Metaanalysis, conclusions and future directions

Considering only studies of lizards that compared behavior and predation pressure on two or more islands or between island and mainland sites,

flight initiation distance was consistently shorter when predation pressure was lower. Depending on the number of comparisons considered to be independent in each study, this was the case for all 10 to 14 cases (1 each for Blázquez et al., 1997; Diego-Rasilla, 2003; Vervust et al., 2007; Cooper et al., 2009b; 3-6 case for Stone et al., 1994; and 2-4 for the combined studies by Berger et al., 2007 and Rödl et al., 2007). Even using the minimum number of independent comparisons, the binomial probability is 0.0020, two-tailed (table 2 using shows the minimum 10 paired comparisons). This appears to be the first comparative demonstration of island tameness with respect to a quantitative escape variable.

When studies of all antipredatory behaviors are included, there are 13-18

independent assessments for at least one variable (the comparisons from studies that reported flight initiation distance plus 1 comparison for Van Damme and Castilla, 1996; 3 for Cooper et al., 2004). These comparisons exclude the numerous comparisons possible between islands in the experimental study by Losos et al. (2004). All comparisons were in the directions predicted from relaxation of predation. Using the minimum number of independent comparisons, the binomial probability that antipredatory traits are equally expressed under conditions of higher and lower predation pressure is 0.00012. When added to the experimental evidence for the effect of an introduced predator on perch height and hind limb length in *Anolis sagrei* (Losos et al., 2004), this finding comparative finding suggests

| Species | Type of comparison | Location | Finding for FID | Source |
|-----------------------------|--------------------------------------|--------------------------------------|----------------------------|-----------------------|
| <i>Ctenosaura hemilopha</i> | island vs. mainland | Gulf of California & Baja California | shorter on island | Blázquez et al., 1997 |
| <i>Podarcis muralis</i> | high vs. low altitude | Cieza Mountains, Iberian Peninsula | shorter at high elevation | Diego-Rasilla, 2003 |
| <i>Podarcis sicula</i> | two islands | Adriatic near Croatia | shorter w. lower predation | Vervust et al., 2007 |
| <i>Podarcis lilfordi</i> | two islands | Menorecan islets | shorter w. lower predation | Cooper et al., 2009 |
| <i>Microlophus</i> spp. | several island pairs in Galapagos | Cerro Colorado vs. Plaza Sur | shorter w. lower predation | Stone et al., 1994 |
| | | Cerro Dragon vs. Venecia | shorter w. lower predation | |
| | | San Cristobal vs. Isla Lobos | shorter w. lower predation | |
| <i>Amblyrhynchus</i> | island pairs in | Caamaño vs. Punta Nuñez | shorter w. lower predation | Rödl et al., 2007 |
| <i>cristatus</i> | Galapagos | Punta Nuñez vs. San Cristobal | shorter w. lower predation | |
| | | Caamaño vs San Cristobal | shorter w. lower predation | |

Table 2. Paired comparisons of flight initiation distance between lizard populations experiencing substantially different levels of predation

that island tameness and associated changes in behavior, physiology, and morphology is a robust and widespread phenomenon.

Several types of evidence strongly suggest that island tameness is a common response to reduced predation pressure. Most prominent among these are (1) the waning of antipredatory behaviors and related physiological and morphological traits related to escape on isolated islands where predators are scarce or absent, and (2) responses of prey species to predators introduced accidentally, intentionally to control rats or other pests, and experimentally. When predators are introduced to such islands, extinctions of prey lacking adequate antipredatory adaptations may occur or antipredatory behavior may become more effective, often rapidly, under selection for predation avoidance. Antipredatory behaviors can be strengthened rapidly by prey under strong natural selection for ability to avoid predation following experimental introduction of predators on islands. Intensity of antipredatory responses also can decline rapidly when predators are removed. The high extinction rate of island reptiles after introduction of mammalian predators provides suggestive, but indirect, evidence that island tameness may be a widespread phenomenon among reptiles.

Most papers relating predation pressure on islands to lizard antipredatory behavior present comparisons among two or three. Studies of lava lizards (Stone et al., 1994), marine iguanas (Berger et al., 2007; Rödl et al.,

2007) and *Anolis sagrei* (Losos et al., 2004; Schoener et al., 2005) are exceptional in that comparisons were made among multiple island populations. Only the experimental studies of anoles provided a number of comparisons adequate to establish an effect of predation on antipredatory behavior across populations. Although the studies comparing two or three populations demonstrated differences in antipredatory behavior as expected if island tameness is a consequence of relaxed predation pressure, each statistically significant finding provides only one to three data points for a comparative evaluation of the relationship.

Comparative studies are time-consuming and may be logistically challenging, but are needed to evaluate the generality and time course of island tameness. Additional experimental studies on effects of introduction of predators are highly desirable. Experimental studies of effects of removing predators would also be informative.

Island tameness refers specifically to reduction of wariness, as indicated by changes in antipredatory behaviors such as vigilance, escape, and refuge use, under relaxed predation pressure on islands, especially isolated islands. However, reduction or elimination of the threat of predation on islands might affect all aspects of antipredatory defense. Isolated studies hint that vigilance (Blumstein et al., 2005) and social defense such as flocking (Beauchamp, 2004) may wane in island populations where selection for

predation avoidance is minimal. Effects of lessened need to avoid predators on isolated islands on many other antipredatory defenses have not been studied to our knowledge.

Reduced predation on islands might lead to reduction or loss of costly chemical defenses, aposematic coloration, mimicry, pursuit-deterrent signalling, death-feigning, deimatic (threatening behavior), preemptive attack, weaponry exaggerated for antipredatory defense, armor, spines, and other defenses. Shifts in diel activity and habitat selection may be expected. If prey are restricted to certain habitats and activity times in the presence of predators, they may be predicted to exhibit ecological release or shifts due to absence of predation on islands. All sorts of morphological and physiological characters maintained by natural selection for predation avoidance (e.g., flat body form to facilitate use of crevices as refuges, endurance to escape from coursing predators) might be modified in the absence of predation. It would seem that there is a research vacuum on such topics. Abundant opportunities exist for fertile investigation of these topics.

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