

# Predation reduces visual communication distance in an *Anolis* lizard

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In his book *Descent of Man and Selection in Relation to Sex*, Darwin (1) made a compelling argument that evolution could not be explained solely on the basis of differential survival (natural selection). In particular, traits that enhance an individual's reproductive success (sexual selection) often decrease its chances of survival. For example, the risks of injury and death can be high for males that fight for direct access to females or for territories that contain resources needed by females. Courtship ornaments and displays, which often determine territorial ownership or mating success, are not only energetically costly but frequently result in increased chances of predation. Some of the most striking and well-documented examples of the latter phenomenon involve reductions in sexual ornaments and modifications of behavior that reduce the conspicuousness of courting individuals in areas where predation is high compared with areas where predators are absent or uncommon (2, 3). These changes

almost certainly increase survivorship at the expense of less effective territorial defense and lower mating success. In PNAS, Steinberg et al. (4) found that males of a semiarborescent lizard, the brown anole (*Anolis sagrei*), on islands in the Bahamas where a predator was introduced show a significant reduction in the amplitude of head bobs compared with lizards from predator-free islands. This behavioral change reduces the communication range of these visual signals, thus lowering the chances of being detected by a predator. By the same token, such signals are likely to be less effective in repelling more distant territorial rivals and attracting potential mates. Whereas a common response to predation is to reduce the duration or frequency of their displays (5), the main change in *A. sagrei* on islands with predators was head-bob amplitude, a display component used in territorial defense and mate attraction.

This behavioral study took advantage of a large-scale experiment on the effects

of introductions of a large predator, the curly-tailed lizard (*Leiocephalus carinatus*) of *A. sagrei* on seven tiny islands (mean vegetated areas of just 250 m<sup>2</sup>) in the Bahamas (Fig. 1). Control islands, lacking predators, had the same area and vegetation profile, and the number of predators introduced was uniformly proportional to the population size of *A. sagrei*. For this study, observations of the behavior of 240 males were made on five islands with predators and four control islands; the displays of 39 of these individuals were videotaped. As in a previous study (6), there was a twofold increase in perch height on islands with predators, which reflects the fact that *L. carinatus* is mostly terrestrial. There was a small decrease in the proportion of time signaling but no difference in the number of head bobs per display. The movement of the head during head-bobs of lizards on islands with predators was about 35% less than that of lizards on predator-free islands. Both kinds of lizards are especially movement-sensitive, especially in the range of visual angles of 0.2–8° (7). Steinberg et al. (4) calculated the distance at which the maximum amplitude of the head bob in each display had a visual angle of 0.2° and, hence, would be expected to optimally stimulate the visual system. These calculations provide estimates of the maximum distance at which the predator and conspecific rivals and potential mates are likely to detect the display. The mean reduction in this “active space” on islands with predators was again 35% (5.8 m vs. 3.7 m on control islands).

The predators were introduced in May 2008, and the data on which this study was based were collected between May 18 and June 11 in 2011. The question then arises: Was this rapid change attributable to phenotypic plasticity, learning, mortality, or some combination of these factors? Steinberg et al. (4) point out that modifying the head-bob amplitude can take place immediately (as opposed to some morphological change) and



**Fig. 1.** Photo of a typical island that was part of a natural experiment. Pairs of such tiny islands, which all had populations of brown anoles (*A. sagrei*), were matched for size and vegetation height. A predator of brown anoles, the curly-tailed lizard, was introduced on one of each pair, and after about 2 y, Steinberg et al. (4) conducted field observations and video analysis of the signaling behavior of brown anoles on islands with and without the predator. Image courtesy of Manuel Leal (Duke University, Durham, NC).

Author contributions: H.C.G. wrote the paper.

The author declares no conflict of interest.

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can be adjusted to a relatively fine degree. Moreover, anoles of another species have been shown to modify their head-bob displays during social interactions with members of the same species (8), and still another anole showed the ability to learn a visual discrimination task in relatively few trials (9). One explanation is that the change is an example of phenotypic plasticity. Brown anoles could have evolved this response to curly-tailed lizards or some other visually orienting predator in the past but were free to use higher-amplitude head-bobs in its absence. Learning is another explanation, which, however, requires a lot of faith in lizard cognitive abilities. An individual would have to experience predation attempts in which it escaped. Subsequently, through trial-and-error, the lizard would have to make and remember the association between reductions in head-bob amplitude and reduced detection by the predator. Finally, the lizard would then have to discount the adverse consequences of reductions in its ability to detect conspecific rivals and potential mates at greater distances. The argument

for mortality as a principal driving force is that predation in this same system resulted in an increase in relative hind-limb length in *A. sagrei* in a matter of 6 mo after the introduction of curly-tailed lizards (6). This change increased running speed on the ground, but a reversal in limb length occurred in a matter of months after *A. sagrei* moved to higher positions in the vegetation (6), as they did in the present study (4). If, as the authors suggest, behavioral plasticity tapping a previously evolved response to predation as well as fine-scale modifications in displays are in the repertoire of this lizard, as in *Anolis grundlachi* (8), then

at least modest differences should be evident in encounters with the predator and those with conspecifics. Steinberg et al. (4) state that they never saw a curly-tailed lizard when they observed and recorded displays of *A. sagrei*; thus some staged encounters would be able to test these ideas (5). Regardless of the factors that brought about the rapid changes in behavior in this lizard, I view these natural experiments in the Bahamas as a gold-mine for discoveries about evolution, not the least of which is the potential for much more rapid adaptive change than expected by many evolutionary biologists.

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