

How the Horned Lizard Got Its Horns

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Many descriptions of evolutionary adaptations are criticized as “just-so stories” (1) that are based more on intuition than on direct tests of adaptive hypotheses. The elaborate crowns of horns possessed by many species of horned lizards (genus *Phrynosoma*) are classic examples of intuitively adaptive features that lack direct tests of function. The bony horns that give horned lizards their name are presumed to function as a defense against predators (Fig. 1B). Here we present data from the wild showing that natural selection by loggerhead shrikes favors longer horns (fig. S1) in the flat-tailed horned lizard (*Phrynosoma mcalli*).

Predation is difficult to document in the wild. Some predators, however, leave behind explicit records of individual predation events that can be exploited to assay natural selection. Loggerhead shrikes (*Lanius ludovicianus*) often impale their prey onto thorns, twigs, and even barbed wire as a means of subduing their quarry (2). When shrikes attack horned lizards, they

typically spear the lizard through the neck and pull off the soft tissue. What remains is a record of the successful shrike predation attempts marked by desiccated skulls of horned lizards hanging in trees and bushes (Fig. 1A).

We quantified selection (3, 4) on relative horn lengths of flat-tailed horned lizards by comparing the skulls ($n = 29$) of shrike-killed lizards with the heads of live lizards ($n = 155$). Our results showed predation by loggerhead shrikes generated selection that favored longer parietal and squamosal horns (Fig. 1, C and D). The average parietal horn length of live horned lizards was 10.0% longer ($\bar{x} \pm SE : 9.65 \pm 0.01$ mm) than that of shrike-killed lizards (8.77 ± 0.21 mm), and the average squamosal horn length was 10.4% greater in live lizards (24.28 ± 0.21 mm) than in those killed by shrikes (21.99 ± 0.49 mm). Visualization of the selection function indicates that both traits experience positive directional selection with threshold lengths above which predation is rare or absent. Standardized selection gradients

[measured in standard deviation units (3)] suggest that selection is stronger on the length of squamosal ($\beta' = 0.0945$; $P = 0.007$) than on the length of parietal horns ($\beta' = 0.0549$; $P = 0.055$). These magnitudes of selection are less than the median observed in most selection studies ($\beta' = 0.15$) (5) but nonetheless indicate that constant selection with moderate heritability (0.5) of horn length would change squamosal and parietal horn lengths a full standard deviation in 21 and 36 generations, respectively.

Modern methods for analyzing natural selection have increased our understanding of which traits experience selection (6). These methods, however, typically cannot identify agents of selection or reveal the functional relations that result in natural selection (3). Even most classic data sets demonstrating selection in the wild, including Bumpus's sparrows (7) and Lande and Arnold's pentatomid bugs (8), did not reveal the agents responsible for the observed patterns of survival. Our results present a rare opportunity to link the statistical form of selection to an identifiable agent, in this case predation by shrikes. Our study does not show that other agents and forms of selection do not play a role in the evolution of horn size, but clearly illustrates that defense against shrike predation is one factor driving the radical elongation of horns in some species of horned lizards.

References and Notes

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Supporting Online Material

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Materials and Methods
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Fig. S1
References

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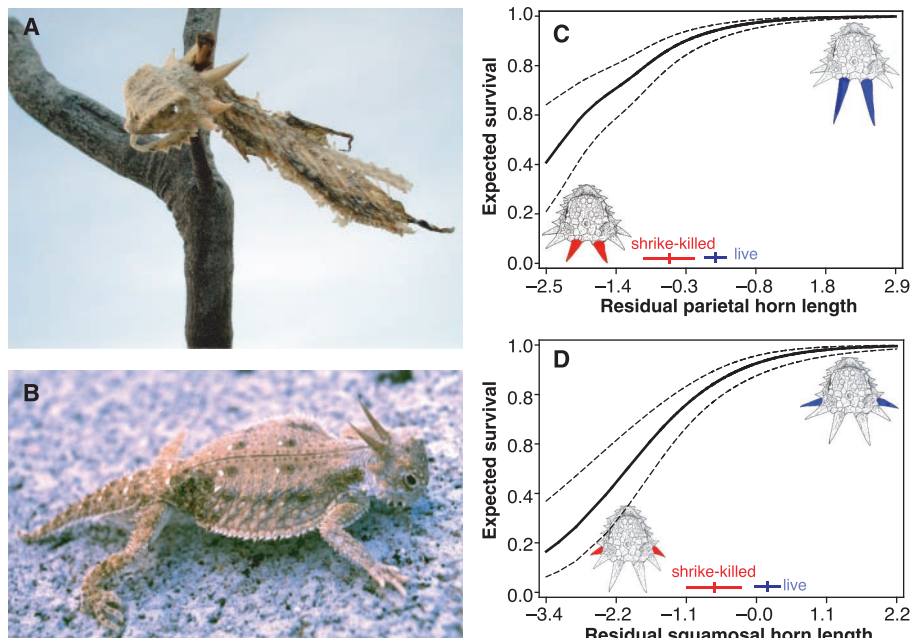


Fig. 1. (A) Flat-tailed horned lizard skull and dorsal skin impaled on a branch. [Photo, E. D. Brodie Jr.] (B) Live flat-tailed horned lizard in defensive posture. [Photo, K. V. Young] The live lizard in this photo had unhealed wounds anterior to the rear legs, consistent with an unsuccessful attack by a predator. Selection surfaces showing relations between survival probability and (C) relative parietal horn length and (D) relative squamosal horn length. Bars show means and 95% confidence intervals for shrike-killed and live lizards.

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