How Did the Horned Lizard Get Its Horns?

IN THEIR BREVIA "HOW THE HORNED LIZARD got its horns," K. V. Young *et al*. present an important example of natural selection in the wild, suggesting that loggerhead shrike predation drove the evolution of elongated horns in the flat-tailed horned lizard (2 Apr., p. 65). Although the authors acknowledge that selective forces other than shrike predation may also be involved, they make no mention of the possibility that one of these potential forces could have been the first instigator of the directional selection for horn elongation. Under this hypothetical scenario, the horns would have then only subsequently served to reduce shrike predation. Other likely cases of preadaptation [or exaptation (*1*)] have been described in vertebrates (*2*–*5*), some of which involve important transitions in evolutionary history. Perhaps the role of preadaptation in evolution is of great importance and is deserving of more widespread appreciation. Given the possibility of a preadaptation scenario in the evolution of crown horns in horned lizards, I find it ironic that Young *et al*. commented on the weakness of "just-so stories" (*6*) and also chose a title that reads remarkably like the titles of Kipling's stories. Until presented with evidence suggesting that the horns were mere nubs until the onset of shrike predation, I will remain convinced that "How the horned lizard got its horns" is a poor choice for what is presumably meant to be an informative title.

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6. R. Kipling, *Just So Stories* (Doubleday, New York, 1902).

IN THEIR BREVIA "HOW THE HORNED LIZARD got its horns" (2 Apr., p. 65), K. V. Young *et al.* claim to have direct evidence of the defensive function of the long bony horns that fringe the lateral and posterior margins of the head of the flat-tailed horned lizard (*Phrynosoma mcalli*). They show elegantly and convincingly that loggerhead shrikes (*Lanius ludovicianus*) prey on lizards with relatively short horns (corrected for body size) and that this source of mortality produces directional selection favoring longer horns. Unfortunately, the authors incorrectly conclude that "defense against shrike predation is one factor driving the radical elongation of horns in some species of horned lizards." This conclusion is incorrect because they did not show that the lizards use their horns to defend themselves against shrikes, nor did they show that longer horns are better for defense. Suppose that lizards with longer horns also are more vigilant, escape faster, spend less time in the open, are more cryptic, or have other traits that reduce the chance they are seen, caught, killed, and eaten by shrikes. Any of these correlated traits could also explain the observed pattern of predation and selection. Observations of how shrikes attack lizards and how lizards defend themselves, and measurements of predation rates on lizards with experimentally shortened and lengthened horns are needed to test the validity of the intuitively attractive suggestion that the horns of horned lizards are defensive. At present, this explanation for the adaptive function for horns remains a "just-so story."

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IN THEIR BREVIA "HOW THE HORNED LIZARD got its horns" (2 Apr., p. 65), K. V. Young *et al*. explain the causal processes of how the flat-tailed horned lizards (*Phrynosoma mcalli*) developed parietal horns as a defense against the impaling capabilities of the loggerhead shrike (*Lanius ludovicianus*). However, the actual selection factor that the horns help to defend the lizards from—how shrikes kill their vertebrate prey—was not discussed. Shrikes prey differentially on invertebrates and vertebrates. A shrike (*Lanuis* spp.) kills its vertebrate prey (*1*, *2*), including species that may weigh as much as an adult shrike (30 to 75 g depending on the species of shrike), with a bite directed at the portion of the prey's neck immediately posterior to the skull. The bite disarticulates the vertebral column. When the prey is dead, a shrike will fly to a convenient perch where the prey is either impaled on a sharp point or dragged and lodged into a fork of a branch (*3*). This allows a shrike to pull the prey apart with its bill into portions that can be swallowed.

Flat-tailed horned lizard in defensive posture.

Natural selection can only occur if individuals survive a given experience and are able to transmit that information to conspecifics or their progeny (*4*). Given my long experience in the field with shrikes, the attack period is the only possible event when a horned lizard could experience and escape the attacks of the shrike to the nape. Further, it is also possible that attacks by inexperienced juvenile shrikes, allowing for a greater percentage of escapes (*3*), on the horned lizards gave rise to the selection for elongated horns. It also does not make evolutionary sense for a trait to be incorporated into a prey species, as a result of a predator's behavior, that results in all cases in its death (i.e., the impaling stage). Hence, although I accept the authors' conclusion that "defense against shrike predation is one factor driving the radical elongation of horns," I suggest that the parietal horns developed as a defense against shrike attacks to the nape region and not against their being impaled after they are dead. Thus, the posterior-directed (and perhaps even the lateral-directed) cranial horns of a *Phrynosoma* lizard are a potential danger to a shrike, aimed as they are at a shrike's eye when it goes in for a lethal bite at the lizard's neck.

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ADVERTISER	Page
Bio-Rad Laboratories	1978
Biosearch Technologies, Inc.	1983
Ciphergen Biosystems, Inc.	1981
Genetix	1984

Turn to page 1979

Response

THE TITLE OF OUR PAPER WAS MEANT AS AN allusion to the *Just So Stories* of Kipling (*1*), which are often used as a shorthand criticism for unsubstantiated adaptive arguments. It is a bold statement, and we thought it so clearly over the top that it would not be taken as a literal explanatory title. The problem of identifying adaptations and their causes has (at least) two schools of thought, one that focuses on the source of the original character state change (as described by Fouts), and one that focuses on current value and selection (as described in our Brevia). Heritable traits that have current adaptive value, as is the case for the horns of flat-tailed horned lizards (*Phrynosoma mcalli*), will continue to change through natural selection, thereby leading to continued adaptation and explaining in part how horned lizards got elongated horns. The question of whether any horns on the head of horned lizards existed before shrike predation drove them to elongated states (i.e., were "preadapted") is an interesting one, but one that is only answerable through comparative analyses with full phylogenetic information and ancestral environmental conditions (*2*). Although we have not performed such an analysis and could probably never reconstruct the ancestral predation conditions, it is worth noting that of the 13 species of horned lizards currently extant, *P. mcalli* has the longest relative horn lengths and belong to the most derived species group (*3*, *4*), while some other species in the genus (e.g., *P. douglassi*) have virtually no parietal or squamosal horns (i.e., the nubs mentioned by Fouts).

Christy correctly points out the two primary shortcomings of any covariance analysis of selection: It is impossible to rule out every unknown unmeasured character that could drive the observed selection, and covariance analyses usually cannot assign a mechanism of selection because they are not manipulative studies (*5*). In the case of shrike predation selecting on horn length in lizards, however, we have measured a fitness component undeniably assignable to predation by a single predator. We also know that lizards routinely use their horns behaviorally in defense, jabbing them backward into anything that restrains them, often with enough force to draw blood from human fingers. It seems most parsimonious to conclude that the fitness advantages conferred by longer horns with respect to shrike predation accrue because of their defensive function, rather than to invoke some unknown correlated character that generates the observed covariance.

Yosef describes the predation behavior of shrikes attacking their prey and in doing so explains some of the critical natural history driving the natural selection we observed. We regret that space limitations prevented us from fully describing the fascinating behavior of shrikes, and the comments of Yosef help to fill in some of these blanks and support the interpretations in our paper. The impaling behavior of shrikes provides a unique sampling of successful predation, but we never intended to imply that horn length served to prevent the impaling process per se.

The defensive behavior of flat-tailed horned lizards is consistent with the interpretation that longer horns deter attacks by shrikes. When attacked or grasped, flat-tailed horned lizards stab their spines into the offending object. In the case of human fingers, this behavior often results in bleeding and immediate release of the lizard. The predation behavior of shrikes, which typically attack near the neck, would place vulnerable areas of the predator's face within range of the parietal and squamosal horns of flat-tailed horned lizards. Lizards with relatively longer horns would be expected to be more likely to be able to reach and inflict damage on a predator, thereby interrupting the predation sequence and escaping.

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The Importance of Educating Girls

IN HIS EDITORIAL "SUSTAINABLE DEVELOPMENT" (30 Apr., p. 649), J. Sachs eloquently describes scientists' increasing concern about the difficulty of providing for a growing global population in sustainable ways.

It will be much easier to achieve decent, sustainable living standards if population growth slows more rapidly. Extensive research from diverse countries shows that while family planning and basic health care clearly play major (and reinforcing) roles, expanding education for women where female education levels are now relatively low is probably the single most effective way to encourage a shift to smaller, healthier, and better educated families (*1*,