Comment on "How the Horned Lizard Got Its Horns"

Recently, Young *et al.* (*1*) purported to identify the mechanism behind the origin and maintenance of horns in horned lizards (Phrynosomatidae: *Phrynosoma*) by demonstrating directional selection for increasing horn length in one population of *Phrynosoma mcalli* from the southwestern United States. In drawing their conclusions, Young *et al*. asserted rather than demonstrated the current function of the trait of interest (that is, they assumed that horns are an antipredatory defense mechanism). In addition, Young *et al.* assumed that current function reflects past selection. In doing so, they have failed to recognize the crucial distinction between adaptation and exaptation (*2*, *3*). These criticisms could have been avoided had the authors given due consideration to the phylogenetic definition of adaptation (*3*–*5*), which uses robust criteria for identifying adaptation.

Numerous definitions of adaptation have been proposed, including adaptation as a process and adaptation as a state of being (that is, current utility and current fitness). Neither definition acknowledges the historical aspect of adaptation (*2*). An adaptation is any feature of an organism that enhances current fitness and whose modification was a result of selection for its current role. In contrast, an exaptation is a trait that has current utility but that did not arise as a result of selection for its current role (*2*, *3*). In this view, an adaptation is a statement about the origin and maintenance of a trait. Brandon (*4*) suggested four criteria necessary to identify adaptation in this operational framework: 1) evidence that selection has occurred on the trait in question, 2) existence of a functional explanation for putative fitness differences associated with the trait, 3) evidence for heritability of phenotypic differences corresponding to trait variation, and 4) knowledge of phylogeny such that putative adaptations can be shown to have originated in selective regimes in which they are currently advantageous.

The explanation provided by Young *et al.* for the origin and maintenance of large horns in *Phrynosoma* satisfies potentially only one of the criteria cited above. Their data show that for one population, lizards with proportionally shorter horns for their body size experience a higher probability of mortality from one predator, loggerhead shrikes (*Lanius ludovicianus*), than do lizards with proportionally longer horns (criterion 1). Although they provide no evidence for heritability of horn length (criterion 3), assuming rather than measuring heritability is a common practice in studies of adaptation, and we do not criticize the authors on this rather strict criterion. More important, they argue that horns protect *P. mcalli* from predation by shrikes but provide no direct evidence of this (criterion 2). Unlike snakes that ingest the entire lizard, shrikes impale horned lizards on branches and do not ingest the spiny head (*1*). Because the predatory event does not involve ingestion of the head, the functional significance of a 10% difference in size-adjusted horn length to a shrike is not at all clear. Currently, horns may function as an antipredator defense mechanism in *P. mcalli*; however, such a function has not been demonstrated in the context of predation by shrikes or any other organism. Moreover, many animals are known to prey on horned lizards, including other lizards, snakes, mammals, and birds (*6*–*8*). The authors relied on finding the carcasses of impaled lizards with heads intact, but because lizards ingested by other predators were not observed (and thus their horn lengths could not be measured), the relative strength of selection on horn length in *P. mcalli* by shrikes (or any other predator) is unknown.

The use of size-adjusted horn length is also problematic. Avian and mammalian predators need not consume the head of horned lizards. Snakes and lizards, on the other hand, generally cannot dismember their prey and must consume the entire prey item. Consequently, they are gape-limited predators. For such predators, absolute rather than proportional or size-adjusted horn length likely determines whether the head can be ingested. Risk of injury resulting from attempts to swallow the head of horned lizards may deter such predators. However, that risk is likely the result of horn configuration (e.g., orientation and absolute size) rather than proportional length. We also note that inferring the functional importance of a trait based on evidence of directional selection is ad hoc. In the case of horned lizards and loggerhead shrikes, behavioral tests and observations of the putative function are needed to support the claim that horn length (especially size-adjusted horn length) directly affects predation by shrikes.

Finally, even if the current functional role of a trait is known, the question of the origin of this trait remains unanswered, which leads to criterion 4 of the phylogenetic definition of adaptation. Without additional evidence, any trait whose current function is advantageous (i.e., affects current fitness) is equally likely to have been coopted for its current function (exaptation) as selected for its current function (adaptation). To distinguish adaptation from exaptation, some knowledge of phylogenetic history coupled with a reconstruction of past selective regimes is needed. Young *et al.* address neither of these issues and, in the absence of proper phylogenetic analyses (*3*, *5*), their conclusions remain speculative. For example, it is plausible that horns arose in the context of sexual selection or crypsis (*9*, *10*) and only later functioned in defense against predators. The data of Young *et al.* cannot refute either of these alternative hypotheses. Inability or failure to distinguish between these two alternative hypotheses is the essence of "just-so stories" (*11*) and is precisely what prompts criterion 4 of the phylogenetic definition of adaptation.

The elaborate horny protrusions on the skulls of horned lizards are a synapomorphy of this monophyletic clade (*12*, *13*) that naturally lead to questions concerning the origin and maintenance of this conspicuous trait. Although we agree with Young *et al.* that the origin and maintenance of horns in *Phrynosoma* is a question of much interest, we argue that the explanation they have provided fails to meet the criteria for identifying adaptation and ignores three decades of discussion of the problems associated with the adaptationist paradigm. Therefore, the question implied in the title of their article—how the horned lizard got its horns—remains unanswered and, in the absence of an historical perspective, is unanswerable.

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