

Response to Comment on “How the Horned Lizard Got Its Horns”

Agosta and Dunham (1) argue that our study (2) did not consider the phylogenetic definition of adaptation and therefore cannot reveal the origin of horns in the larger group of horned lizards. Because we neither presented phylogenetic evidence nor made claims about the historical origin or past selection on horns in this group, this criticism is generally accurate, if somewhat extraneous. We suspect that the misunderstanding stems from the paper’s title, which was meant as a humorous allusion to the just-so stories of Kipling (3) rather than as a literal description of our work. We expected that the title’s intent would be clear and regret that we confused some readers. A more accurate title, perhaps, would have been “How the Flat-Tailed Horned Lizard Got Its Long Horns.” Our brief article (2) addressed only the current function and adaptation of horn length in modern populations of the flat-tailed horned lizard and clearly stated that “[o]ur study does not show that other agents and forms of selection do not play a role in the evolution of horn size.” Nonetheless, the critique by Agosta and Dunham (1) does underscore the contentiousness of concepts of adaptation, as well as the inability of either ecological or phylogenetic approaches to the problem to fully satisfy all critics.

Agosta and Dunham argue that we have not demonstrated adaptation of horned lizard horns and could not do so without a phylogenetic perspective. This interpretation is based on a historical definition of adaptation that emphasizes the exaptation/adaptation dichotomy (4–6). This is one important aspect of adaptation, but not the only one (7, 8). In the parlance of Gould and Vrba (4), and those that followed, an exaptation differs from an adaptation in that the former is a feature whose “origin cannot be ascribed to the direct action of natural selection” for its current use. Subsequent attempts to outline methodology for distinguishing exaptation from adaptation (5, 6, 9, 10), including the four-part paradigm repeated by Agosta and Dunham, have used phylogenetic frameworks to determine when a character changes state in relation to the selective environment. Although the historically based definition of adaptation has been productive, and we wholeheartedly support its application, we also believe that the blind subscription to this ideal as the only way to understand the phenomenon of adaptation is limiting and

masks important aspects of the process of adaptation in natural populations.

First, the process of evolution, and as a part of it adaptation, is dynamic and continuous. A purely historical perspective on adaptation obfuscates the reality that selection continues to occur and modify phenotypes in a way that leads to increased fitness. Historical definitions of adaptation include current selection (9, 10) but commonly view it as a force that maintains a character state and increases fitness by eliminating less fit mutations. However, directional selection of the sort described in our paper actually changes the state of a character and thereby is a force generating adaptation. As pointed out by Price in his famous covariance equations (11), selection can be defined as a statistical relation between phenotypic variance and fitness. The extension of this relation to evolutionary theory (and before that to artificial selection by way of the “breeders’ equation”) demonstrates that current selection on any heritable trait leads to phenotypic change (12). For the flat-tailed horned lizard, selection by shrikes leads to a covariance between survival probability and horn length. This selection alone would lead to a change of approximately 10% in only 20 to 30 years, assuming a moderate heritability. Certainly many biologists would view such a phenotypic change as an example of adaptation, regardless of the ancestral origin of horns. To ignore the role of current function in driving adaptation is to assume that evolution is something that has occurred only in the past.

This example also illustrates the second shortcoming of the phylogenetically restrictive definition of adaptation: It is inherently a statement about character states distributed across clades and thus has limited applicability to continuous change on short time scales. Phylogenetic frameworks have been developed to analyze continuous characters, but these necessarily emphasize the contrast between clades and taxa rather than observable change through time within a given lineage (10, 13). Empirical studies of evolution have repeatedly demonstrated “rapid” phenotypic change over a time scale well short of that observable in a phylogenetic context (14), and geographic variation within species often equals or exceeds what is present among clades (15, 16). If we focused only on phylogenetic patterns of phenotypic change, we would never have learned that a

few generations of altered selection regime can dramatically change the life history of guppies (17), the shape of finch bills (18), or the mating morphology of salmon (19). In the case of horned lizards, analyses at both phylogenetic and contemporary levels undoubtedly will be productive. Species of horned lizards within the genus *Phrynosoma* vary greatly in the size and shape of horns emanating from the skull. The most derived species group within the genus includes three of the species with the longest relative horn sizes (20, 21). Of these taxa, the flat-tailed horned lizard has the longest parietal (rear) horns of any species (20), but populations vary. Thus, within the genus *Phrynosoma*, evolution appears to have led to a derived condition of quantitatively longer parietal horns, without a change in character state of presence or absence of these horns. The historical forces that led to this quantitative elaboration of horn length are lost to us; even the strongest historical reconstructions of selective context are at best correlative and speculative regarding how selection operated at some point in deeper phylogenetic time (22). It is clear, however, that selection by shrikes generates the relationship necessary to continue to drive the elongation of horns in the short term.

The very definition of exaptation leads to a third problem with the historically based definition of adaptation. Because selection is a process that works with available material and existing variation only, all character states that are modified by natural selection by definition already exist in a population. By the strict application of Gould and Vrba’s original definition, all traits could be labeled exaptations if we look at a generation-by-generation process [although Larson and Losos (10) disagree, preferring to call such traits “nonaptive or disaptive”]. New mutations arise before selection can act upon them, yet few would be expected to spread through a population if selection did not favor them. On the other hand, if current selection leads to the modification of traits, such as shrike predation driving the elongation of horns in flat-tailed horned lizards, then selection is in fact altering the trait as required by the strict definition of adaptation. If we look at biodiversity through a diffraction lens that only allows us to see discrete differences in character state or species identity, then it appears that the distinction between current and past function is clear. However, if we study selection at a microevolutionary level, this distinction becomes more arbitrary. Much as the disagreement over punctuated equilibrium as an evolutionary process reduces to a perspective of time scale and consequent questions (23), the issue of adaptation versus

exaptation depends on the scale of biodiversity and evolutionary time that we seek to explore.

Finally, Agosta and Dunham offer some criticism of the interpretation of current function that we do present in our paper. They argue that we are unsuccessful in identifying the function of horned-lizard horns because we do not know why the covariance between horn length and survival exists. As with all non-manipulative studies of selection, this is strictly true (24). However, in this case we believe that we have strong inferential evidence. Behavioral observations of flat-tailed horned lizards captured in the wild reveal that individuals twist their heads to the back or side to drive their parietal or squamosal horns into any physical restraint (e.g., human fingers, forceps). The horns are sharp enough and the defensive behavior vigorous enough that in many cases lizards draw blood from “attacking” human fingers. Paired wounds and scars from presumed bird attacks on the bodies of some live lizards (illustrated in figure 1B of Young *et al.*) further suggest that this sort of behavior is effective in successfully deterring predation attempts. The most reasonable explanation for why shrikes kill relatively short-horned individuals is that they are less effective at deterring predation than are their longer horned conspecifics. Agosta and Dunham further criticize the use of size-adjusted horn length in our analysis because shrikes do not consume the heads of lizards. In the behavioral scenario described above, it is actually relative, not absolute, horn length that matters, because this measure determines how much of its vulnerable neck region—the favored attack site of shrikes (25)—a lizard can protect with its horns. A large lizard with large absolute horns but short horns relative

to its body length might not be able to stab an attacking bird, but still might deter a gape-limited predator, as suggested by Agosta and Dunham. In any case, the purpose for analyzing relative horn length was to be conservative and eliminate the possibility that we would confound selection against small lizards with selection against small horns.

We believe we have presented a compelling example of selection in action, and one that identifies an agent and cause of selection that leads to adaptation (2). Contrary to the comments of Agosta and Dunham (1), our paper did not attempt to distinguish adaptation from exaptation or to reveal the ancestral origin of the horns in the genus *Phrynosoma*. Although we find the historically based definition of adaptation useful in many cases, and suspect that it will be a productive direction of research on horned lizards, we do not believe that it is obligatory or even relevant in all cases, nor should it be exclusive of studies of current function. Microevolutionary studies of the continuing process of natural selection are just as important to understanding how adaptation occurs as are the macroevolutionary studies that reveal their distribution in time and phylogeny.

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