LIZARD LOCOMOTION: HOW MORPHOLOGY MEETS ECOLOGY

by

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ABSTRACT

Biological evolution often leads, through natural selection, to an optimal fit between 'design' and ecology. However, the adaptation process may be impeded or slowed down by several constraints or trade-offs between conflicting functions. This is frequently observed by ecomorphological studies focusing on lower taxonomic levels: form-function relationships get blurred because subtle adaptive traits remain hidden or simply do not exist. Therefore, a rigorous analytic approach is required, (ideally) assessing the links between the four stages of the adaptive process simultaneously (i.e., from genetic variation to variation in design, to variation in performance, to differential fitness), taking into consideration all potential factors hindering the normal progression of this process. Lizard locomotion is a good model for such an analysis. Locomotion is essential in many ecologically relevant functions (feeding, predator avoidance, etc.). It consists of several components (speed, acceleration, endurance, manoeuvrability, etc.) and modes (level running, climbing, etc.) with conflicting demands, leading to potential trade-offs. Moreover, several of its components proved to be heritable and obvious relations between habitat use and locomotor design are often absent (e.g., in lacertid lizards). Two cases, focusing on the potential trade-off between climbing and level-running, are presented to illustrate the subtle interplay between variation in ecology, performance and design in lizard locomotion. (1) For two gekkotans (a climber and a ground dwelling species) the moments exerted by several important leg muscles appear to be tuned to their primary mode of locomotion. (2) In two sibling lacertid species, the inverse trade-off between climbing and running, put forward on the basis of observed substrate use, does not exist. Instead, a drastic difference in running performance, likely related to different running styles, emerged. The latter case illustrates the potential use of 'integrated, dynamic design traits' as an intermediate stage between variation in design and performance.

KEY WORDS: adaptation, locomotion, lizards.

INTRODUCTION

The great extent to which organisms are adapted to the tasks they have to fulfil in their specific environment has always been a subject of

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wonder and biological study. Pre-darwinian thinkers, from Aristotle to William Paley, considered this proof for the existence of a divine designer. Ironically, DARWIN (1859) turned the same match between form and function into one of the most powerful arguments for the existence of natural selection and its importance in biological evolution.

Over a wide taxonomical range, relationships between biological form and ecology are very often obvious and convincing. A classical example are the forelimbs of mammals, which evolved from a primitive state into wings in bats, spades in moles, running legs in antelopes, peddles in dugongs and so on, leaving no doubts about the adaptive nature of these evolutionary modifications.

Focusing onto lower taxonomic levels (e.g., family level), however, the nice tight fit between the form and the ecological function frequently gets blurred or seems even not to exist. The degree to which morphological diversification tracks ecological radiation appears to be highly taxon-dependent. For instance, the morphological adaptation coupled to the trophic radiation of the cichlid fishes (COULTER, 1991) or Darwin finches (LACK, 1947; GRANT & GRANT, 1982; BOAG & GRANT, 1984; SCHLUTER & GRANT, 1984; SCHLUTER et al., 1985) sharply contrasts with the high morphological resemblance of the sympatric Pomatoschistus minutus and lozanoi, sand gobies with different feeding niches (HAMERLYNCK, 1990; HAMERLYNCK & CATTRIJSE, 1994; own observations) or with the absence of a correlation between morphology and diet in grassland birds (WIENS & ROTENBERRY, 1980). Similarly, while adaptation to habitat use has lead to clearly distinguishable eco-morphs in Anolis lizards on each of the major islands of the West Indies (COLLETTE, 1961; WILLIAMS, 1972; MOERMOND, 1979; LOSOS 1990a, b, c; 1992; LOSOS et al., 1994; LOSOS, 1995; LOSOS et al., 1998), the rather uniform appearance of lacertid lizards seems, at first glance, not to reflect the variable demands imposed by the diverse habitats these animals are living in (ARNOLD, 1989). The absence of a correlation between design and ecology may result from the adaptive traits being hidden or too subtle to be revealed by the applied analytic tools, or from actual constraints (environmental, historical, etc.) that slow down or prevent the proper progress of the adaptation process, thus disturbing the relation between form and function (GOULD & LEWONTIN, 1979; REEVE & SHERMAN, 1993; RIDLEY, 1993; WINSOR, 1993; DENNETT, 1995; SIH & GLEESON, 1995; FUTUYMA, 1998). If correlations between form and ecological niche do show up, proper testing of the adaptive nature of the traits remains a prerequisite. Emerging correlations can be non-adaptive for the function considered (for instance, when specialisation for climbing makes new food sources available, differentiation of the jaw apparatus