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Shaping intraspecific variation: development, ecology and the evolution of morphology and life history variation in tiger salamanders

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Abstract

The tiger salamander, *Ambystoma tigrinum*, is a geographically widespread, morphologically variable, polytipic species. It is among the most variable species of salamanders in morphology and life history with two larval morphs (typical and cannibal) and three adult morphs (metamorphosed, typical branchiate, cannibal branchiate) that vary in frequency between subspecies and between populations within subspecies. We report morphometric evidence suggesting that branchiate cannibals arose through intraspecific change in the onset or timing of development resulting in the wider head and hypertrophied tooth-bearing skull bones characteristic of this phenotype. We also quantified bilateral symmetry of gill raker counts and abnormalities, then evaluated fluctuating asymmetry as a measure of the developmental stability of each morph. There was a significant interaction between fluctuating asymmetry of developmental abnormalities in cannibals and typicals and the locality where they were collected, suggesting that relative stability of each phenotype could vary among populations. While altered timing of developmental events appears to have a role in the evolution and maintenance of morphs, novel phenotypes persist only under favorable ecological conditions. Predictability of the aquatic habitat, genetic variation, kinship, body size, intraspecific competition and predation all affect expression and survival of the morphs in *A. tigrinum*. This taxon provides an excellent model for understanding the diversity and complexity of developmental and ecological variables controlling the evolution and maintenance of novel phenotypes.

Introduction

Simultaneous occurrence of two or more distinct morphs of a species is a polymorphism if the rarest type is not maintained by recurrent mutation (Ford, 1965). Within the context of the Evolutionary Synthesis, 'conspicuous polymorphisms' (Wright, 1968), such as whole body color, were used to study ecological and genetic factors associated with the origin and maintenance of discontinuous variation in general (e.g., Dobzhansky, 1937), and some kinds of geographic races in particular (e.g., Mayr, 1942). Wright (1978) noted that such polymorphisms are interesting as adaptations and easy to study, but he relegated them to a peripheral role in evolution arguing that they are not typical of the variation on which evolution depends. There may be conditions, however, under which a conspicuous polymorphism could play a significant role in rapid phyletic divergence (Mather, 1955; Alexander & Bigelow, 1960; West-Eberhard, 1986). Stanley (1979: 171-172) elaborated this argument: 'A basic question is how much of the ultimate variability that emerges in adaptive radiation arises as polymorphism within the original species, perhaps later to be fixed by the interposition of breeding bar-

riers... Rapid divergence in this scheme, though preceding reproductive isolation, would still occur almost simultaneously with it on a geologic scale of time, making the described mechanism a form of quantum speciation. Thus, I am in agreement with other authors (Eldredge & Gould, 1972; White, 1978, p. 9) that the quantum morphologic step may commonly predate a population's attainment of formal status as a discrete species.'

West-Eberhard (1986) proposed an 'alternative-adaptation hypothesis' linking conspicuous intraspecific polymorphisms and speciation. Once alternative phenotypes become established in a population, she argued, ecological conditions can then arise that favor only one form. Release of the genome from constraints of accommodating multiple alternatives then facilitates speciation by accentuating divergence from the original population. Ultimately, a new lineage emerges that is characterized by the newly fixed and modified form. West-Eberhard provided several reasons to consider this model. First, speciation via this scheme could be frequent since intraspecific alternative phenotypes are more common than is usually realized as exemplified by protozoa, rotifers, mites, insects, birds, amphibians, mammals, fungi, and higher plants. This hypothesis also provides a clear framework in which to explore the relationship between ecology, development, and evolution. Finally, her model suggests mechanisms for understanding how natural selection can favor the evolution of 'macroevolutionary' changes in design, including phylogenetically important changes caused by heterochrony (Stanley, 1979; Wright, 1982). Heterochrony is phyletic change in the onset or timing of development, so that appearance or rate of development of a feature in a descendant ontogeny is either accelerated or retarded relative to appearance or rate of development of the same feature in an ancestor's ontogeny (Gould, 1977).

The tiger salamander, *Ambystoma tigrinum* (Green) has a distinctive, complex, polymorphic life history which, it is believed, has been strongly influenced by heterochrony (Gould, 1977). This taxon is one of about 113 species of salamanders with a distinct larval stage in the life cycle. In about 42 of these species (37%), some or all adults in a population are morphologically identical to larvae, but larger, and termed adult branchiate morphs. In most of these 42 species, this morph and a mature

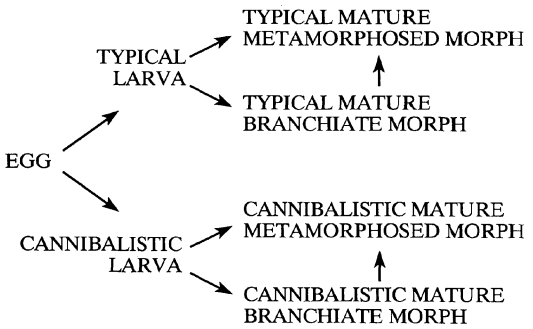

Fig. 1. Summary of variation in life history and morphology in *A. t. nebulosum* or *A. t. mavortium*, subspecies in which cannibalistic larvae and branchiate adults occur regularly.

metamorphosed morph occur in the same population. *A. tigrinum* is unique among these 42 species in that four subspecies each have two juvenile morphs as well (Fig. 1). Some populations of *A. t. mavortium* Baird, *A. t. nebulosum* Hallowell, *A. t. tigrinum* Dunn, and *A. t. melanostictum* Baird have typical larvae and cannibalistic larvae (Powers, 1903, 1907; Gehlbach, 1967; Lannoo & Bachmann, 1984; Rilley, Lauder & Collins, 1992).

Our objective in this study was twofold. First, we sought to analyze the role of changes in developmental timing in the origin of this complex polymorphism. Several arguments suggest mature typical branchiate morphs have evolved via 'intraspecific heterochrony', where juvenile characters are retained by adult ontogenetic stages. We tested the hypothesis that branchiate cannibals also have evolved through delayed differentiation relative to typical larvae. Second, we evaluated the developmental bases of the polymorphism. If the evolutionarily derived cannibalistic phenotype evolved via a disruption of the developmental program of animals with a typical morphology, then cannibals could be viewed as abnormal morphological deviants, or 'phenodeviants' (Lerner, 1954). We used departure from bilateral symmetry as a measure of developmental stability, or homeostasis, of typical and cannibal phenotyes. The cannibals, as phenodeviants, would be expected to exhibit a disruption of bilaterally symmetrical expression of morphometric traits.