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Trophic Polymorphisms, Plasticity, and Speciation in Vertebrates

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Abstract. Trophic polymorphisms are relatively common among vertebrates. In this chapter I review the occurrence of trophic polymorphisms among vertebrates, discuss what is known about the cause of these polymorphisms, enumerate the unifying ecological and morphological factors among the examples, and present a qualitative model of intraspecific trophic divergence where plasticity in combination with other factors can lead to sympatric reproductive isolation of the morphs. Trophic polymorphisms are found in all classes of vertebrates; however, they are most common among lacustrine fishes. Although little information is available about the relative contribution of genetic and environmental factors to the polymorphisms, data indicate that phenotypic plasticity alone could be responsible for the differences between morphs in many of the cases. The characteristics that unify the cases are as follows: (1) animals use only their mouths to subdue, capture, and process their prey; (2) there are two or more food types or suites of food items (e.g., zooplankton vs. benthic invertebrates) in different habitats that require different modes of capture or processing; (3) there is sufficient behavioral flexibility to take advantage of the multiple prey types; (4) the prey populations are temporally stable; and (5) the polymorphic species occur in relatively species-poor environments characterized by some empty niche(s).

In cases where the above five factors are satisfied, morphological divergence and, ultimately, speciation can occur via the following pathway. Behavioral plasticity can lead to foraging specialization. Foraging specialization can, in turn, lead to morphological differences as the result of morphological plasticity. These morphological differences reinforce the foraging specialization by changing the relative foraging efficiencies of the two morphs on the different food types. Induced morphological differences can affect mate choice or nesting habitat preference, or, if the polymorphism is habitat-based (e.g., the common limnetic/benthic polymorphism found in some temperate fishes), it can affect timing of spawning. When this sequence of events occurs, partial reproductive isolation can occur in a single generation solely as the result of behavioral and morphological plasticity. For the morphs to become significantly reproductively isolated, there also needs to be philopatry among the young to the parents' foraging ground or food type.

Introduction

Trophic polymorphisms (polymorphisms related to diet) and variation are intriguing because they provide the potential for intraspecific niche differentiation and, ultimately, speciation (Mayr 1963:

Rosenzweig 1978; Wilson 1989). In addition they provide an unparalleled opportunity to examine ecological phenomena such as competition and predation without the confounding effects of different phylogenetic histories. By polymorphism, I mean the occurrence of more than one discrete phenotype in a population (Mayr 1963, "old" definition), including both genetically and environmentally determined phenotypic differences, because for many instances the genetic and environmental contributions to the phenotypic differences are unknown. Some of the polymorphisms described below are discrete only when combinations of continuous morphometric characters are analyzed multivariately.

Polymorphisms can result from genetic influences, environmental influences, or a combination of both. For instance, flight polymorphisms in insects can be completely environmentally determined, under simple genetic control, or be the result of genotype-by-environment interaction (Harrison 1980; Roff 1986). Most characters are influenced by both genetic and environmental factors; different characters of an individual can vary in the amount of plasticity they express, and different genotypes can exhibit different amounts of plasticity in response to a range of environments.

In this chapter I first review the available literature on vertebrate trophic polymorphisms and the relative contributions of genetic and environmental factors to the polymorphisms. Next, the ecological correlates of the polymorphisms and the potential of trophic polymorphisms and variation, including that due to plasticity, to contribute to speciation are discussed. The evidence for the sympatric or allopatric origin of morphs where partial to virtually complete reproductive isolation has occurred is also discussed. For this reason some problematic examples of species complexes have been included where morphs in some populations may actually represent different biological species. This review is restricted to trophic characters and excludes color and meristic polymorphisms, and polymorphisms attributable to sex, age, or size differences because these have been previously reviewed and do not necessarily have the same causes or evolutionary implications (Barlow 1961; Selander 1966; Polis 1984; Werner and Gilliam 1985).

Trophic Polymorphisms and Variation in Vertebrates

The following section describes vertebrate trophic variation and polymorphisms. I have included a few examples of trophic variation that may not satisfy the requirements of discrete phenotypes within a population because the organisms illustrate trophic partitioning and correlated morphological and behavioral differences between morphs.

FISHES

Whitefishes

Coregonine fishes of the family Salmonidae provide a striking example of the problem that morphological polymorphism can present to systematists and ultimately to any biologist working on a polymorphic system. The whitefish genera (*Coregonus* and *Prosopium* spp.) are found in temperate lakes throughout the Holarctic. Scattered throughout their range are numerous lakes where two or

more forms of what appear to be a single species coexist. For instance, over 800 lakes in Sweden have more than one morph of whitefish living in sympatry (Svärdson 1979). Whitefish morphs are usually characterized by differences in gill raker number and length, often accompanied by differences in body shape and mouth position. Gill rakers enhance the capture of small food particles, such as zooplankton (Sanderson et al. 1991). Zooplanktivorous (limnetic) whitefish tend to have longer and more numerous gill rakers than those that feed on benthic organisms or insects. Of characters shown to vary between morphs, gill rakers are thought to be the morphological character most canalized (buffered) against environmental influence (Svärdson 1952, 1979; Kliewer 1970) although even gill rakers are somewhat susceptible to environmental modification (Koelz 1929; Kliewer 1970; Lindsey 1981). Other characters such as relative body size and shape dimensions are sensitive to both environmental and genetic influences (Svärdson 1949, 1970). For instance, Svärdson (1970) showed that dwarf morphs transplanted into fishless lakes grow larger and develop relatively different head and body dimensions than their dwarf counterparts. The directions of shape change parallel those expected from functional considerations. Fish feeding on more evasive prey, such as zooplankton, tend to have more fusiform bodies whereas fish feeding on stationary, benthic prey generally have deeper, rounder bodies (Webb 1984).

In North America the best known example of trophic polymorphism involves the lake whitefish, *Coregonus clupeaformis* (Mitchill). There are two forms in at least five lakes in Maine (Fenderson 1964), Opeongo Lake in the Ottawa-St. Lawrence drainage (Kennedy 1943), Squanga Lake and four others in the Yukon (Bodaly et al. 1988), and several lakes in British Columbia (McPhail and Lindsey 1970). The sympatric forms are a dwarf and a normal form. In four Maine lakes the dwarf has the higher gill raker count, and in the fifth lake the dwarf is bimodal with respect to gill raker count. However, in Opeongo Lake the dwarf morph has a lower gill raker count (Lindsey et al. 1970). In Squanga Lake and three other lakes in the Yukon, the dwarf form has more gill rakers (Bodaly et al. 1988) and is the zooplanktivore. Lindsey (1981) suggests that the high-rakered forms are usually dwarfed due to the relatively low abundance of zooplankton in northern lakes.

McCart (1970) documents the existence of two forms of the pygmy whitefish, *Prosopium coulteri* (Eigenmann & Eigenmann), in Alaska. One form is characterized by lower number of gill rakers, a subterminal mouth, concave head profile, deeper body and caudal peduncle, smaller orbit, and a less compressed body than the high-rakered form. Stomachs of the high-rakered form, as one might expect, were full of zooplankton whereas low-rakered forms fed primarily on bottom fauna. The two forms are spatially separated in lakes with the high-rakered fish found in depths <10 m and the low-rakered form found deeper. The two forms may spawn at slightly different times. The morphological differences found in two-morph lakes are not useful in identifying morphs when they exist in allopatry, suggesting that character displacement may be occurring in two-morph lakes.

Svärdson (1957, 1970, 1979) describes six to seven different forms of whitefish in Sweden. Many lakes contain two forms, and one lake contains five different morphs. Again, gill raker number in combination with size, spawning time, or color are the primary characters used to distinguish forms or species.

The differences between morphs usually involve a large suite of characters important in food capture, some of which are more or less canalized than other characters within the same organism. For instance, gill raker number in whitefish is more canalized than head and body shape measures (Svärdson 1979). So, for whitefish species, even where morphs within lakes are partially reproductively isolated, the relative influence of genotype and environment differs for every character examined.

Charr

Perhaps the best studied group of trophically polymorphic vertebrates, Arctic charr, *Salvelinus alpinus* (Linnaeus) (also in the family Salmonidae), comprise a complex of landlocked and anadromous populations found in lakes throughout the Holarctic. At least seven species have been described, but many, if not most, have been classified as morphs of a single polytypic species (Johnson 1980). Up to four morphs coexist in some lakes (e.g., Thingvallavatn Lake in Iceland), but usually only two forms—a dwarf and normal morph—coexist in a single lake (reviews in Balon 1980; Johnson 1980; Hindar and Jonsson 1982; Johnson and Burns 1984). These forms are characterized by differences in number of gill rakers, pyloric caecae, life history characters, color, body proportions, and diets. Usually the dwarf form is a midwater fish that feeds on zooplankton and is characterized by more gill rakers, a more pointed snout, and a larger eye, whereas the normal form feeds on benthic organisms (Johnson 1980). This pattern is reversed in some lakes and may be a function of the relative abundance of zooplankton and benthic organisms. Sometimes an additional anadromous morph is also present. Examples of polymorphism abound in lakes throughout northern North America, Europe and the CIS (formerly the Soviet Union) (Johnson 1980).

The most dramatic example of polymorphism is found in Thingvallavatn Lake, Iceland, where three or four forms of *S. alpinus* coexist (Hindar et al. 1986; Jonsson et al. 1988; Skúlason et al. 1989): a small benthivore, large benthivore, a planktivore and a piscivore. Using detailed life history data, Jonsson et al. (1988) found evidence that all four morphs are partially reproductively isolated. In a breeding experiment, Skúlason et al. (1989) found evidence for only three genetically distinct morphs; the piscivore appears to be a planktivore that has become big enough to eat sticklebacks.

The basis of morphological differences among charr morphs may be different in different drainages. In a breeding experiment using charr from the Salangen River, Norway, Nordeng (1983) found no evidence for genetic control of morph differentiation because each morph had offspring of all morphs.

Goodeids

In some rivers in Mexico, a narrow-mouthed fish originally described as *Ilyodon furcidens* (Jordan and Gilbert) is sympatric with a broad-mouthed fish originally described as *Ilyodon xantusi* (Hubbs and Turner 1939). Narrow-mouthed morphs possess rounded jaws, a narrow gape, and several rows of teeth whereas the broad-mouthed morphs possess squared jaws, a broad horizontal gape, and reduced or absent inner rows of teeth. Narrow-mouthed morphs also tend to have fewer teeth and gill rakers than broad-mouthed morphs (Turner and Grosse 1980). The dietary basis of the polymorphism is unknown. Turner and Grosse (1980) collected electrophoretic data indicating the two "species" were actually two morphs of a single species. Turner et al. (1983) did further electrophoresis and showed extensive differentiation among localities, but no differentiation between morphs from a single locality. Grudzien and Turner (1984) raised broods of fish for which the morphs of both parents were known and performed both heteromorphic crosses and homomorphic crosses. The young were fed a combination of brine shrimp nauplii and flake food. All but one homomorphic cross resulted in progeny of the opposite morph from the parents. None of the laboratory-raised young developed mouths as broad as field-collected, broad-mouthed fish. Also, a greater proportion of intermediate morphs occurred in the laboratory-reared fish than in the field-caught fish.

These results indicate a great deal of variation in trophic morphology in *Ilyodon*; however, they do not conclusively demonstrate plasticity. In order to show plasticity, sibs need to be raised on different diets. In addition to detailing the extent of plasticity, many questions still remain. On what do the different morphs feed? Why do some drainages contain monomorphic populations and others dimorphic ones? Does the absence or presence of other species "allow" the dimorphism to occur, or does it occur only in certain habitats? How stable is the dimorphism in a population over ecological and evolutionary time scales?

Sticklebacks

Threespine sticklebacks, *Gasterosteus aculeatus* Linnaeus, exhibit a limnetic/benthic polymorphism in some lakes in British Columbia, similar to the polymorphisms described for charr and whitefish. In Enos Lake, British Columbia, the limnetic (pelagic) morph is characterized by a relatively shallower body; longer and shallower head; longer snout, upper jaw, and gill rakers; and a bigger eye (McPhail 1984). Limnetics feed primarily on zooplankton, and benthics feed primarily on benthic invertebrates (Bentzen and McPhail 1984). The polymorphism in Enos Lake has a definite genetic basis. McPhail (1984) found that homomorphic crosses only resulted in offspring with parental phenotypes, whereas heteromorphic crosses resulted in F1s with intermediate morphology. The two morphs choose different habitat types (Bentzen et al. 1984), show almost perfect assortative mating, and build their nests in different places (Ridgway and McPhail, 1984). Studying a similar polymorphism in a different lake, Larson (1976) showed that benthics dominated limnetics in social interactions.

Schluter and McPhail (1992) reported that in all five two-morph lakes they examined the morphological and morphometric differences between morphs were bimodally distributed. Morphology and gut contents were highly correlated. Limnetic fish had zooplankton in their stomachs, and benthic fish were filled with benthic invertebrates. Mean morphological measurements of fish from one-morph lakes were intermediate to the means of benthics and limnetics from two-morph lakes. However, within single-morph lakes there was fairly good correspondence between the presence of zooplankton in a fish's stomach and its gill raker length. This observation indicates some ecological structuring even within single-morph lakes. Whether these differences are due to morphological plasticity in response to primary foraging mode, or are due to genetically determined morphology determining foraging mode is unknown.

Sunfish

Ehlinger and Wilson (1988) found that bluegill sunfish, *Lepomis macrochirus* Rafinesque, caught in the pelagic portion of Holcomb Lake, Michigan, had shallower bodies, shorter pectoral and pelvic fins, and pectoral fins placed more anteriorly than fish caught in the vegetation (limnetic and littoral, respectively). Bluegills caught in the two habitats forage differently: littoral bluegills feed on insects that are relatively cryptic, whereas limnetic bluegills feed on zooplankton that are relatively conspicuous. Littoral bluegills hover longer between movements than those from open water. When littoral bluegills are fed zooplankton in open aquaria, their hover rates decrease, but they still hover longer than limnetic bluegills. Maximum foraging rates in vegetation were positively correlated with