

EVOLUTIONARY SIGNIFICANCE OF RESOURCE POLYMORPHISMS IN FISHES, AMPHIBIANS, AND BIRDS

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ABSTRACT

Resource polymorphism in vertebrates is generally underappreciated as a diversifying force and is probably more common than is currently recognized. Research across diverse taxa suggest they may play important roles in population divergence and speciation. They may involve various kinds of traits, including morphological and behavioral traits and those related to life history. Many of the evolutionary, ecological, and genetic mechanisms producing and maintaining resource polymorphisms are similar among phylogenetically distinct species. Although further studies are needed, the genetic basis may be simple, in some cases under the control of a single locus, with phenotypic plasticity playing a proximate role in some taxa. Divergent selection including either directional, disruptive, or frequency-dependent selection is important in their evolution. Generally, the invasion of "open" niches or underutilized resources requiring unique trophic characters and decreased interspecific competition have promoted the evolution of resource polymorphisms. Further investigations centered on their role in speciation, especially adaptive radiation, are likely to be fruitful.

INTRODUCTION

Resource-based or trophic polymorphisms are likely more common and of greater evolutionary significance than is currently appreciated. Work on diverse taxa suggests that these polymorphisms, in which discrete intraspecific

morphs show differential resource use and often varying degrees of reproductive isolation, may represent important intermediate stages in speciation (14, 150, 190). Many of the mechanisms and conditions that produce and maintain resource polymorphism are similar, even among highly divergent taxa (150). Yet, until recently, little effort has gone toward examining this phenomenon across different taxonomic groups. For example, important studies on resource polymorphisms involving fishes, amphibians, and birds have been published in recent years, but there have been few comparisons of the processes involved (but see 51, 56, 150, 197). In this review we summarize the diverse nature of the phenotypic differences involved, and through selected examples explore the ecological and evolutionary implications of this phenomenon. We hope to promote an integrative cross-taxon approach to the study of resource polymorphisms and greater efforts toward identifying additional examples. Numerous other examples likely exist, but because discrete phenotypes may be subtle, they are easily overlooked or discounted. We do not review sex-based polymorphisms because they are beyond the scope of the present review. We begin by describing the nature of resource polymorphisms in each taxon, then we discuss circumstances and mechanisms maintaining them, and finally we discuss their evolutionary significance.

TYPES OF ALTERNATIVE ADAPTIVE PHENOTYPES

We define resource polymorphisms as the occurrence of discrete intraspecific morphs showing differential niche use, usually through discrete differences in feeding biology and habitat use. Morphs may differ in morphology, color, behavior, or life history traits, and in many instances they may differ in more than one characteristic (Table 1).

Fishes

Many examples of resource polymorphisms appear across diverse fish taxa, including mostly freshwater and anadromous fishes. Resource-based morphs of fishes may differ in behavior, life history, morphology, and color, and they may coexist within the same freshwater system, i.e. they are intralacustrine (155) and may even be found within small landlocked lakes. Frequently, different forms show varying degrees of reproductive isolation, even to the level of being classified as distinct biological species (56, 133, 141). Since the segregation among some of these forms is clearly correlated with resource use and represents part of a continuum, we include them in our discussion.

Resource polymorphisms in fishes are common in lakes in recently (10,000–15,000 years) glaciated areas of the northern hemisphere (127, 141). The arctic charr (*Salvelinus alpinus*), a circumpolar salmonid, often has from two to four sympatric intralacustrine resource morphs. Morphs differ in adult body size and

shape, and in life history characteristics (e.g. 49, 66, 68, 69, 105, 122, 125, 147, 167, 188). In some cases resource segregation is clear and stable, such as between benthic and limnetic habitats (79, 135), while in other cases, habitat and food segregation are less dramatic and often seasonal (57, 125, 168, 188). The degree of phenotypic differences may also differ among lakes (148, 167). For example, in Thingvallavatn, a lake in Iceland where resources are unusually well defined and discrete (67), four morphs display substantial behavioral, life history, and morphological differences (69, 78, 152, 167). The lake has an extensive littoral zone made structurally complex by volcanic substrate. A small benthivorous charr (7–22 cm long) occupies the subbenthic habitat consisting of porous volcanic rubble, while a large benthivorous charr (20–50 cm) occurs in the epibenthic habitat. Both morphs specialize on snails. In addition, there are two limnetic morphs, one smaller (14–22 cm) and planktivorous, the other larger (adults 25–60 cm) and piscivorous (37, 79). The limnetic morphs also have more streamlined bodies, more pointed snouts, and more gillrakers than do the benthic morphs (78, 153, 167). Some spatial and temporal variability in spawning among the morphs can be related to their diet and the availability of spawning grounds (152), and some evidence suggests assortative mating (146). Molecular genetic studies, combined with the distribution of morphs in other lakes, show that the morphs are closely related and arise locally, with benthic forms derived from the more common limnetic form (148, 167; see also 59).

In whitefish (*Coregonus* and *Prosopium* spp.), numerous examples of intralacustrine forms are found in Europe and North America (76, 170). As in arctic charr, the degree of discrete differences among sympatric whitefish forms in resource use and morphology varies among lakes (e.g. 2, 9), but morphs are typically benthic or limnetic. They may differ in adult size and other life history attributes and in morphology such as jaw length and bluntness of snout (76, 83). The number and morphology of gillrakers (associated with type of prey) have most commonly been used to discriminate forms, which can reach five within a single lake (2, 9, 33, 76, 80, 170). An extensive molecular genetic survey in North America suggests that morphs may be genetically divergent within single lakes but do not represent separate invasions from adjacent rivers or lakes (10, 70; but see 5).

The Pacific salmon (*Oncorhynchus nerka*), native to the northern Pacific Ocean, exhibits two morphs, the anadromous sockeye and the nonanadromous kokanee. The former typically spends the first year in a lake before migrating to the ocean, whereas the latter remains in lakes throughout its lifetime (5, 35). Kokanee matures at a smaller body size and often at a younger age than sockeye, and where they coexist, they may display distinct morphological differences such as more gillrakers in the former (35, 99, 198). Kokanee have originated from sockeye independently and repeatedly. For instance, kokanee

Table 1 Resource polymorphisms in selected vertebrate species and the nature of the ecological segregation among morphs

Species	Nature of discrete ecological differences	PD ^a	References
FISHES			
Arctic charr (<i>Salvelinus alpinus</i>)	Benthivory, planktivory, piscivory, and migration	m,b,l	(47, 49, 57–59, 66, 69, 79, 105, 106, 122, 125, 149, 153, 167, 168, 188)
Atlantic salmon (<i>Salmo salar</i>)	Migration	l	(8, 183)
Brown trout (<i>Salmo trutta</i>)	Benthivory, planktivory, piscivory, and migration	m,b,l	(34, 87, 127)
Brook charr (<i>S. fontinalis</i>)	Benthivory, planktivory, swimming activity	m,b	(7, 43, 84)
Sockeye salmon (<i>Oncorhynchus nerka</i>)	Benthivory, planktivory, and migration	m,b,l	(35, 127, 198)
Coho salmon (<i>Oncorhynchus kisutch</i>)	Lake versus stream habitat	m,b	(172)
Lenok (<i>Brachymystax lenok</i>)	Benthivory, planktivory, and piscivory	m,l	(71, 110)
Lake whitefish (<i>Coregonus clupeaformis</i>)	Benthivory, planktivory, piscivory, and migration	m,b,l	(9, 27, 33, 76, 127, 141, 185, 197)
Least cisco (<i>Coregonus sardinella</i>)	Benthivory, planktivory	m,l	(80)
Pygmy whitefish (<i>Prospium coulteri</i>)	Benthivory, planktivory,	m,l	(76, 83, 197)
Scandinavian whitefish (<i>Coregonus</i> spp.)	Benthivory, planktivory, and piscivory	m,b,l	(27, 127, 141, 197)
Rainbow smelt (<i>Osmerus mordax</i>)	Benthivory, planktivory, piscivory, and migration	m,b,l	(175)
Stickleback (<i>Gasterosteus aculeatus</i>)	Benthivory and planktivory	m,b	(23, 86, 127, 141, 197)
Bluegill sunfish (<i>Lepomis macrochirus</i>)	Benthivory and planktivory	m,b	(28, 29, 127, 197)
Pumpkinseed sunfish (<i>Lepomis gibbosus</i>)	Benthivory and planktivory	m	(127, 128, 197)
Tui chub (<i>Gila bicolor</i>)	Benthivory and planktivory	m	(39, 127)
Cichlids (<i>Perissodus</i> spp.)	Eating scales from left versus right side of live fish	m	(63)
Cichlid (<i>Cichlasoma minckleyi</i>)	Feeding on snails and plant material	m,b	(72, 74, 127, 197)
Cichlid (<i>Cichlasoma citrinellum</i>)	Feeding on snails and soft-bodied prey	m,b	(90–92, 127, 197)
Cichlid (<i>Astatoreochromis alluaudi</i>)	Feeding on snails and soft-bodied prey	m	(46, 94)
Goodeid fish (<i>Ilyodon</i> spp.)	Strong indication of differences in food (lake form)	m	(48, 127, 182, 197)

(Continues)

Table 1 (Continued)

Species	Nature of discrete ecological differences	PD ^a	References
Neotropical fish (<i>Saccodon</i> spp.)	Different techniques in eating algae	m	(126, 127)
AMPHIBIANS			
Salamanders and newts			
<i>Notophthalmus v. viridescens</i>	Habitat, metamorphosing	m, l	(55)
<i>N. v. dorsalis</i>	Habitat, metamorphosing	m, l	(53)
<i>Taricha granulosa</i>	Habitat, metamorphosing	m, l	(81)
<i>Ambystoma tigrinum</i>	Habitat/diet, cannibalism	m, l	(19, 22)
<i>A. talpoideum</i>	Habitat, metamorphosing	m, l	(54, 112, 143, 144)
<i>A. lermaensis</i>	Habitat, metamorphosing	m, l	(145)
<i>A. amblycephalum</i>	Habitat, metamorphosing	m, l	(145)
<i>A. rosaceum</i>	Habitat, metamorphosing	m, l	(17, 145)
<i>A. ordinarium</i>	Habitat, metamorphosing	m, l	(3, 145)
<i>A. gracile</i>	Habitat, metamorphosing	m, l	(145)
Frogs and toads			
Spadefoot toad (<i>Scaphiopus multiplicatus</i>)	Omnivory, carnivory, and cannibalism	m, l	(113, 115, 119)
Pacific treefrog (<i>Pseudacris regilla</i>)	Habitat selection by color morphs	m, b	(97)
BIRDS			
Pacific reef heron (<i>Egretta sacra</i>)	Differences in hunting techniques associated with color	m, b	(130)
Little blue heron (<i>Egretta caerulea</i>)	Foraging success and vulnerability to predators	m, b	(16)
<i>Buteo</i> hawks	Proposed differential hunting success of color morphs	m	(129, 131)
Hook-billed kite (<i>Chondrohierax unicinnatus</i>)	Feeding on different size tree snails	m	(164)
Oystercatchers (<i>Haematopus ostralegus</i>)	Different feeding techniques on mussels	m, b	(40, 64, 107, 169)
Woodcock (<i>Scolopax rusticola</i>)	Ecological correlates of different bill types unknown	m	(12)
Blackcap warbler (<i>Sylvia atricapilla</i>)	Differences in migratory behavior	b	(6)
Robin (<i>Erihacus rubecula</i>)	Differences in migratory behavior	b	(6)
Seedcracker (<i>Pyrenestes ostrinus</i>)	Feeding on soft- and hard-seeded sedges	m	(156, 160, 162)
Cocos finch (<i>Pinaroloxias inornata</i>)	Feeding behavior, food type	b	(189)
Darwin's Finch (<i>Geospiza conirostris</i>)	Diet, ephemeral in population	m, b	(44)

^aPD, Phenotypic difference; m, morphological; b, behavioral; and l, life history.

have appeared after sockeye were introduced to lakes previously lacking the species (35). The timing and locality of spawning may or may not differ (73), but molecular genetic studies suggest that distinct genetic differences exist between sympatric morphs (35) and that intralacustrine morphs arise locally (35, 176). In the volcanic lake Kronotskiy in Kamchatka, benthic and limnetic morphs of kokanee differ in the number of gillrakers and show spatial and temporal segregation in spawning (73).

Rainbow smelt (*Osmerus mordax*) exhibit extensive life history diversity throughout northeastern North America. There are both sea-run and lake-resident populations, with the latter often diversified in single lakes into dwarf and normal-sized forms. The dwarf smelt, which is limnetic, has more gillrakers, larger eyes, and a shorter upper jaw than the normal benthic piscivorous form, which is similar in morphology to anadromous smelt (175). In two of the study lakes, molecular genetic analysis showed that forms are reproductively isolated and that the segregation had occurred independently within each lake (175).

The pumpkinseed (*Lepomis gibbosus*) and the bluegill sunfish (*L. macrochiru*) co-occur and occupy distinct niches in many North American lakes. The adult bluegill is an open-water planktivorous generalist, while the pumpkinseed specializes on snails and occurs in shallow water (128). In a lake where the pumpkinseed is rare, a shallow water morph of bluegill is found coexisting with the typical open-water form. The shallow-water morph has a deeper body and longer fins than the open-water form. Clear differences appear between morphs in the flexibility of their feeding behavior, which correlates with differential foraging success in their respective habitats (28, 29). In lakes where only pumpkinseeds occur, they may segregate into two morphs, differing in the structure of gillrakers and body shape; the typical form feeds on snails, and an open-water form seemingly occupies the bluegill niche (128). Morphs tend to breed in somewhat different habitats (128). The phenotypic differences of the sunfish morphs are relatively subtle and went unnoticed in numerous ecological studies (29, 128).

The threespine stickleback (*Gasterosteus aculeatus*) is widely distributed in coastal regions throughout the northern hemisphere, occurring in marine, brackish, and freshwater and expressing a variety of ecological forms. In six small landlocked lakes in British Columbia, Canada, pairs of limnetic and benthic forms coexist, showing a high degree of ecological segregation. The limnetic form is slim-bodied with many long gillrakers and a narrow mouth, while the benthic is larger, deep-bodied, with a few short gillrakers and a wide mouth (86, 88, 140). The pairs show positive assortative mating (86, 124), but there is a persistent low level of hybridization. The forms are thus recognized as good biological species that evolved after the last glaciation (86). Research shows that they may represent two separate invasions that have

subsequently diverged (86), sympatric divergence, or both (177). Benthic and limnetic stickleback morphs were recently identified in a lake in Alaska; they are believed to have arisen sympatrically (23). Morphological differences between them are much less pronounced than those between the species pairs in British Columbia, and the percentage of intermediate forms is much higher.

Cichlid fishes are celebrated for their high species richness in lakes of the African rift and in Central America (27, 38). *Cichlasoma minckleyi* of Cuatro Ciénegas, Mexico, exhibits two morphs, one vegetarian and the other feeding on snails. The former has a narrow head, long intestine, and small papilliform pharyngeal jaw dentition. The latter has short intestines, a wider head, stouter jaw, and larger molariform pharyngeal teeth, used for crushing snails (72, 74, 134). That the morphs interbreed is clear from molecular genetic and spawning ground studies (72, 134). Behavioral trials show that feeding segregation of morphs is most pronounced when resources are limited (74). Another cichlid (*Cichlasoma citrinellum*) has similar morphs in Nicaraguan lakes, as does an African cichlid (*Astatoreochromis alluaudi*) found in East Africa (46, 90–92). In general, variability in jaw morphology is frequently noted in African cichlids (197), and it has been suggested that some of the numerous species that have been described in the African lakes represent resource morphs (72, 94). A clear case of resource polymorphism with little or no genetic isolation is seen in the scale-eating cichlid *Perissodus microlepis* in Lake Tanganyika. Morphs exhibit right- and left-handedness in jaw morphology; the former removes scales from the prey's left side, while the latter removes scales from the prey's right side (63).

Amphibians

Studies investigating adaptive plasticity in amphibian metamorphosis have provided important information on the relative costs and benefits of alternative adaptive phenotypes (20, 101–104, 192). Amphibians may be polymorphic with respect to metamorphosis, with some populations exhibiting both aquatic and metamorphosed adults (3, 17, 102, 144) (Table 1). Larval morphs may differ in numerous cranial and postcranial structures such as teeth, jaw musculature, and body size (11, 109, 197), intestine length (115), and age and size at metamorphosis (22, 115), some relating to whether they are carnivorous (often cannibalistic) or omnivorous.

In the New Mexico spadefoot toad (*Scaphiopus multiplicatus*), rapidly developing cannibalistic morphs grow larger than more slowly developing omnivorous morphs. Carnivorous tadpoles differ from typical omnivorous larvae in their hypertrophied jaw musculature, fewer teeth, decreased melanization, and shorter intestine (109, 119). All these characteristics may be induced during metamorphosis in anurans by exposing them to thyroid hormone (31, 36, 50, 52).

Polymorphisms in trophic structures also occur in some subspecies of larval and adult tiger salamanders (*Ambystoma tigrinum*) (18–20, 22, 118, 120, 132). Morphs may differ in maturation patterns; these may include retention of larval characteristics at sexual maturity in aquatic habitats (paedomorphosis via neoteny), or metamorphosis and sexual maturation in terrestrial habitats. Larval forms include “typical” morphs, which feed on zooplankton and other invertebrates, and cannibalistic morphs, which feed on both invertebrates and conspecifics (20, 22, 60, 77, 118). Relative to the typical morph, cannibalistic morphs are characterized by broader heads and mouths with enlarged vomerine teeth, adaptations apparently evolved for feeding on conspecifics (22, 118). Three morphs occur in adults, including metamorphosed, typical branchiate, and cannibal branchiate (21, 22), but there are few studies showing ecological differences among these morphs. Many species of *Ambystoma* vary in their propensity to metamorphose (Table 1), a variation resulting in obvious differences in resource use (terrestrial vs aquatic). For example, most *A. talpoideum* larvae metamorphose into terrestrial juveniles or adults, while in other populations individuals retain a larval morphology and reproduce as paedomorphs (112, 142).

That some color polymorphisms include a resource component has also been documented. These involve predation avoidance and use of differing microhabitats by being cryptic, although such examples are somewhat more difficult to demonstrate (100, 121, 180). For example, microhabitat selection by green and brown color morphs of the Pacific tree frog (*Pseudacris regilla*) appears to occur in response to predation (97).

Birds

Trophic morphs in birds may show differences in morphology, behavior, or a combination of both (Table 1). Bill-size morphs of the African finch *Pyrenestes ostrinus* feed on sedge seeds which differ in hardness. Morphs with small bills feed more efficiently on soft seeds, while the large-billed morphs do so on hard seeds (157–163). Studies of reproductive behavior indicate that finches mate randomly with respect to bill size (156, 157, 163). Different bill types of the hook-billed kite (*Chondrohierax uncinatus*) appear to be related to feeding on different size/age classes of tree snails (164), while in the oystercatcher (*Haematopus ostralegus*), differences in bill morphology are correlated with differences in feeding behavior and arise by differential wear of the bill. “Stabbers” have pointed bills and feed on mussels by inserting their bill between the valves, while “hammerers” exhibit blunt bills and break shells open by pounding (40, 107, 169). The frequency of morphs may also change seasonally as a function of differential wear imposed by dietary switches (64). An example of a behavioral polymorphism that has given rise to differential discrete niche use

is seen in the Cocos Island finch (*Pinaroloxias inornata*). While the population exhibits little morphological variation, individuals show a diverse array of feeding behaviors, equivalent to those of several families of birds (189). The common color polymorphisms in herons may be maintained by differences in morph crypticity related to foraging mode (61, 98). Differences in habitat and foraging mode have been best documented between morphs of the Pacific reef heron (*Egretta sacra*), in which dark morphs employ a “standing and waiting” or “running mode” in shallow water, while the white phase employs a “flight-freeze” in breaking surf. It is believed that the white phase is more cryptic to prey in breaking surf and the dark phase more so in shallow, calmer waters (130). Experimental evidence for differential hunting success of color morphs is presented by Mock (96). Mock found that more fish were captured near models of white herons than around dark herons when the models were placed in shallow water on sunny days where herons typically forage. This experiment supports the assertion that the white form is more cryptic to fish when viewed against a clear sky. In general, however, although color polymorphisms are widespread in birds (15, 65), relatively few examples exist in which color morphs use resources differently.

Behavior polymorphisms with a demonstrated genetic basis include migration tendency in populations of two European birds, the blackcap (*Sylvia atricapilla*) and the robin (*Erithacus rubecula*) (6). Some populations show bimodality in migration behavior, in which some individuals are resident and others are migratory. While the evolutionary significance is unclear, it is likely to be resource-based (6). Some resource polymorphisms may be ephemeral in nature, such as in the case of the Darwin’s finch, *Geospiza conirostris*, on the island of Genovesa in the Galápagos Islands (41, 44, 45). Males during one season were found to exhibit two discrete song types, while the male of each type differed in bill length and foraging mode. Longer billed, song A males, fed on *Opuntia* cactus flowers, whereas shorter billed, song B males, spent more time feeding on rotting *Opuntia* pads where they obtained larvae and pupae. While some initial evidence suggested assortative mating, morphological differences soon disappeared through random mating (41, 42).

ECOLOGICAL CIRCUMSTANCES THAT PROMOTE RESOURCE POLYMORPHISMS

Open Niches, Habitat Variability and the Relaxation of Interspecific Competition

From the examples discussed thus far, two circumstances appear fundamental in promoting resource polymorphisms: the existence of “open niches” or

underutilized resources, and a relaxation of interspecific competition. Resources in many young lakes in the northern hemisphere are discrete, and fish tend to occur in either benthic or limnetic habitats (127, 141). For example, pumpkinseed and bluegill sunfish occupy distinct ecological niches where they co-occur; however, where only the pumpkinseed occurs, it has differentiated into two morphs (128). In whitefish the presence of competition may be inferred from morphology (76). Limnetic morphs of *Coregonus* with high gillraker counts are not found where the highly specialized cisco (*Leucichthys*) is present, and limnetic forms of *Prosopium* are not found where both of the other genera are present (76). Similarly, morphs of arctic charr are found where competing species are few or absent (78, 122). For instance, in Iceland, where only three species of fish are common in lakes, unusually diverse arctic charr morphs have evolved, taking advantage of most available habitats and resources (79, 127, 148, 152, 153, 167). Similarly, typical and cannibal morphs of tiger salamanders occur primarily where resource competitors and potential predators (fish) are relatively few (22). The lack of interspecific competition and the occurrence of an "empty niche" is also likely operating in the endemic Cocos island finch. Existing on an isolated oceanic island, much like a species of fish existing in a landlocked lake, and lacking interspecific competitors, this finch has diversified intraspecifically, exhibiting an array of distinct foraging behaviors typical of different species (189).

Habitat diversity and distinctness of resources can play an important role in fostering resource polymorphisms. For instance, volcanic lakes offer diverse and complex benthic habitats, often associated with subbenthic spaces, fissures, and caves rich in invertebrate prey for fish to exploit. Trophic adaptations in benthic charr morphs are clearly associated with subbenthic volcanic habitats (135, 148, 167). It is probably therefore not a coincidence that fish morphs and recently evolved species flocks are often found in volcanic-, rift-, and crater lakes as well as in recently deglaciated lakes (27, 67, 72, 93, 95, 137, 155, 167).

The Role of Specialization

Resource polymorphisms may also arise in some species-rich environments if resources are unique and require specialized traits to use. This appears to be the case in the finch *Pyrenestes ostrinus*, in which each morph specializes on sedge seeds differing in hardness, even though they occur in equatorial Africa, a region rich in granivorous birds species (156, 160–163). In this case, the resource on which these finches specialize is not used by other species. Cracking hard sedge seeds requires very specialized, broad, stout bills that sympatric granivorous species lack (162, 163). Because the most closely related species of finches have small bills, similar in size and shape to the small morph, it is believed that larger billed morphs have evolved from small billed forms by specializing on harder

seeded sedge species (162). This is similar to the situation in the oystercatcher in which initial specialization on intertidal mussels seems to have given rise to even greater specialization, resulting in discrete feeding modes and a dimorphism in bill morphology (40). Another example in which specialization may lead to utilizing new resources is seen in the Lake Tanganyikan scale-eating cichlid fish (62, 63). Morphs are either left-handed or right-handed in the direction of mouth opening. In all three instances, specialization is associated with utilizing new, previously underexploited, resources.

Behavioral specialization of individual fish (cf 25), even at a very early age, may play an important first step in segregation. For example, variability in early behavior in the Atlantic salmon influences foraging and thus growth and later life history (88, 178); varying levels of flexibility in foraging behavior have been identified as key features in some polymorphic systems (7, 28, 29, 43, 47, 79, 84, 89, 90, 153, 197).

MECHANISMS MAINTAINING RESOURCE POLYMORPHISMS

Modes of Selection

Disruptive and frequency-dependent selection may play important roles in maintaining resource polymorphisms. A dramatic example of frequency-dependent selection is found in the Lake Tanganyika scale-eating cichlid fish. The frequency of right-mouthed and left-mouthed morphs fluctuated around a ratio of 1:1 over a ten-year period. Apparently individuals of the rarer morph are at a selective advantage because they are more successful in snatching scales from the flanks of prey (63). In New Mexico, omnivorous and carnivorous larval morphs of the spadefoot toad coexist in ephemeral ponds. Because of its faster developmental rate, the carnivorous morph is favored in short-duration ponds, but in longer-duration ponds, the slower-developing omnivorous morph is favored because its larger fat reserves enhance postmetamorphic survival. In ponds of intermediate duration, the abundance of each morph is frequency dependent (113, 115, 119).

In the African finch, *Pyrenestes ostrinus*, disruptive selection is most intense in juveniles (158, 161). Fitness peaks are associated with small and large morphs and correspond to performance peaks on soft- and hard-seeded sedges (162). In these finches, individuals at the extremes of each morph exhibit lower feeding performance and survival. Selection appears to be most intense following the major dry season, when food availability is low (160, 161).

Studies on the limnetic and benthic pairs of threespine stickleback in British Columbia show that the different forms have relatively higher feeding

performances and grow best in their respective habitats, while hybrids do poorly in either habitat, suggesting selection against hybrids (139). Similarly, studies of early development suggest that hybrids of sockeye and kokanee suffer higher mortality than do pure lines (198). Behavioral studies on other fish species almost exclusively show that performance of each morph is positively correlated with the resource it utilizes (28, 29, 78, 90, 153, 193). In general, divergent selection (selection against intermediates) in the evolution of sympatric morphs and/or new species of freshwater fish is likely the result of intraspecific competition for food between phenotypically similar individuals. Subsequent, increased phenotypic divergence of sympatric forms would lead to reduced competition between them (74). This has recently been thoroughly discussed in the context of character release and displacement (127, 138, 140, 141, 173).

Phenotypic Plasticity, Induction, and Genetic Basis

Distinct morphological phenotypes may result from phenotypic plasticity (136, 184, 191). For example, cannibalistic and paedomorphic morphs of tiger salamanders and spadefoot toads arise through a developmental response to varying densities of conspecifics and food type (19, 111, 113–115, 117, 119). In tiger salamanders, morphogenesis is also responsive to kinship, with mixed broods more likely to develop the cannibal morphology than full-sib groups (116). Similarly, food type and quality change trophic morphologies in species of cichlid fishes (89, 194–197) and in pumpkinseed sunfish (187). In fishes, varying degrees of plasticity in foraging behavior and technique within and among morphs (28, 29, 74, 78, 90, 153) may lead to greater morphological specialization, which in turn channel the array of behavioral possibilities (90, 197). Similarly for oystercatchers, behavioral flexibility in feeding on discrete resources results in a bill dimorphism (40, 169). Life history among morphs is often highly plastic in fish, depending on food and habitat (58, 106, 151, 165, 166, 186). Such differences may depend on variability in foraging and social behavior, even very early in life (47, 88, 178).

The relative contribution of heredity and environment to phenotypic differences in fishes seems to vary not only among species but also among populations. The relative contribution varies among lakes in arctic charr (58, 106, 149, 151, 153, 171) and, based on rearing experiments, among forms in whitefish and Mexican *Ilyodon* (179). In contrast, morphological differences in species pairs of threespine sticklebacks in British Columbia have a strong genetic component (85, 86), but environmentally induced effects on morphology may accentuate their segregation. In the wild, the limnetic form has a more variable diet than the benthic form, and this is associated with relatively greater morphological plasticity in the former (24). Similarly, it is likely that both

foraging behavior and growth patterns are less plastic in small benthivorous charr than in planktivorous charr in Thingvallavatn (78, 151, 153). The latter occupies a more temporally unstable niche than does the former, and long-term life-history studies of planktivorous charr show great fluctuations among year classes in growth and maturation patterns (165, 166).

In general, the genetic basis behind most resource polymorphisms is poorly understood. Both the bill size polymorphism in *Pyrenestes ostrinus* and handedness in the scale-eating cichlids appear to be determined by one locus with two alleles (63, 162). Moreover, the simple genetic control of at least some polymorphisms suggests that reaching new adaptive peaks may occur through mutations of large effect (108). To what extent other resource polymorphisms are controlled by one or a few loci will require further study.

While most alternative morphs are conditional and nonreversible, a few show reversible plastic phenotypes (90, 91, 115). In the cichlid *Cichlasoma citrinellum*, individual morphology may change reversibly in different seasons, depending on the kind of food available (91), a situation similar to that found in the oystercatcher, discussed earlier. While switches based exclusively on phenotypic plasticity seem to have evolved in unstable environments (22, 106, 115), switches under strong genetic control (63, 156, 158, 160, 162, 163) seem to evolve under relatively more stable environmental conditions. However, the determination of the role and importance of environmental stability requires further work. For example, common garden experiments involving the salamander *Ambystoma talpoideum* suggest that some populations have evolved phenotypic plasticity with respect to the tendency to metamorphose as ponds dry, while others show a genetic polymorphism (54, 144).

The developmental patterns producing different morphs also need further study. In several cases, heterochrony (1) has been emphasized (4, 22, 89, 149). A release from developmental and/or functional constraints can partly explain why some species are polymorphic and others are not. It has been suggested that a release of functional constraints in the jaw structure of cichlids allowed diversification in their feeding behavior, and that this partly explains their extensive radiation (75, 89, 90). In this case, phenotypic plasticity could either increase the rate of speciation or buffer against extinction, both leading to a net increase in species over time (89).

Alternative Adaptive Phenotypes and Speciation

The potential role resource polymorphisms play in speciation has been debated for decades (13, 14, 32, 51, 82, 94, 156, 190, 191). Most models and much of the debate center on whether the ecological separation caused by resource polymorphisms is sufficient to promote assortative mating and reproductive isolation in sympatry (14, 32, 82). Most alleged examples of sympatric speciation

are correlative in that sympatric speciation is inferred from the dispersion pattern of already discrete species or races, as in some insects (174). A convincing example in vertebrates is found in some cichlids from Cameroon, West Africa (181): Mitochondrial DNA analysis of cichlid species flocks endemic to two crater lakes strongly suggests that each lake contains a monophyletic group of species that originated sympatrically (137). Species within lakes are more closely related to each other than they are to riverine species or species from adjacent lakes, and there are no geographic features of the lakes that could have provided geographic isolation. While polymorphisms were not demonstrated in this instance, they are likely to have been an intermediate step, given the many lakes in East and West Africa that contain polymorphic populations of cichlids (93, 95).

The amount of gene flow among sympatric morphs is variable and, if restricted, may lead to divergence and speciation (10, 34, 35, 56, 59, 87, 175–177). This may occur through either postzygotic mechanisms such as reduced fitness of hybrids (90, 94, 139, 198) or prezygotic mechanisms such as spatial and temporal segregation in breeding (often promoted by philopatry) and differences in breeding behavior or mate choice (9, 26, 27, 33, 80, 86, 91, 94, 124, 128, 132, 146, 152, 155, 175). These kinds of isolating mechanisms may coevolve with the phenotypic attributes such as size and color and the ecological segregation that characterize adaptations of morphs in their respective subniches (27, 91, 93, 128, 146, 152, 155). Among freshwater fish populations, segregation has occurred repeatedly within the same freshwater system and even within the same lake (10, 35, 56, 59, 86, 175), and the degree of genetic divergence between sympatric morphs is highly variable. In some cases, gene flow may be unimpeded, while in others, sympatric types may appear partially or completely reproductively isolated (10, 34, 56, 59, 86).

Niche-specific adaptation, typical of resource polymorphisms, is a key element in the divergence with gene flow speciation model (30, 32, 123, 154). A recent review (123) of laboratory studies involving *Drosophila* finds considerable support for the model when positive assortative mating occurs as a by-product of pleiotropy and/or genetic hitchhiking. The model proposes that speciation may occur under a range of selection intensities and levels of gene flow lying along a continuum: At one extreme is a population in a homogeneous environment with selection for two opposing phenotypes, and at the other extreme are parapatric populations experiencing differing directional selective forces in each. Reproductive isolation occurs if traits important in isolation are correlated or if they are the same as the traits important in resource use. Rice & Hostert (123) refer to this as the single-variation model of divergence-with-gene-flow speciation. In the model, reproductive isolation

evolves through pleiotropy and/or genetic hitchhiking (sampling error–induced linkage disequilibrium between alleles affecting positive assortative mating and alleles affecting divergently selected characters) (123). Particularly salient is that a complete barrier to gene flow is unnecessary for speciation to occur if selection is strong and the trait under selection is also important in reproductive isolation. One could imagine just such a situation if morphs tended to reproduce where they fed and discrete resources occurred in different habitats. We believe this model has particular merit in understanding the possible role of resource polymorphisms in speciation. Incorporating aspects (Figure 1) of this model, resource polymorphisms could lead to speciation in the following steps: (a), (a), . . . , 1) invasion or exploitation of new or unexploited resource (“open” niches), 2) a decrease in intraspecific competition, 3) multifarious (usually divergent)

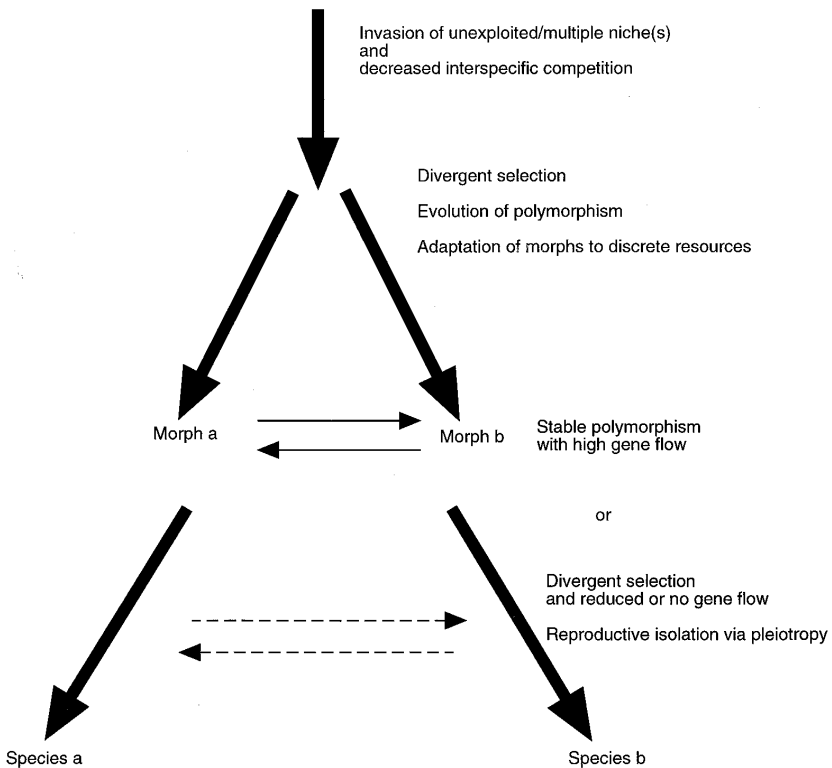


Figure 1 Generalized schematic showing possible steps and mechanisms leading to resource polymorphisms and speciation.

selection and evolution of a polymorphism, and 4) reduced gene flow and the evolution of prezygotic reproductive isolation mechanisms (150). If the model proves correct, as laboratory studies suggest, perhaps the reason resource polymorphisms not more common is that they more likely lead to speciation than to stable polymorphisms.

CONCLUDING REMARKS

Resource polymorphisms have been largely underestimated as a diversifying force and are likely more common and important in speciation than is currently appreciated. Many of the mechanisms that produce and maintain resource polymorphisms are similar among diverse taxa. Recognizing that many of the differences that separate morphs may be subtle, but nevertheless discrete, will likely lead to identification of more examples, especially in taxa where there is a tendency to assume that discontinuous morphotypes represent distinct species. The respective roles of development, phenotypic plasticity, genetics, natural selection, and ecology in maintaining and producing resource polymorphism, and a consideration of why polymorphisms appear more common in some taxa than others are fruitful areas for further investigation.

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