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Resource polymorphisms in vertebrates Skúli Skúlason and Thomas B. Smith

Recent research on a number of vertebrates shows that resource-based or trophic polymorphisms are widespread and diverse. Morphs have often clearly evolved and coexist in sympatry. These studies are making important contributions to our understanding of phenotypic plasticity, mate recognition, competition, niche use, natural selection, population divergence and speciation¹⁻⁹.

Despite an increasing number of examples (Table 1) and many striking similarities between distantly related species, there have been few attempts at cross-taxon comparisons. The fish literature is particularly rich with examples of resource-based or trophic polymorphisms (hereafter resource polymorphism), but few authors compare their systems with those found in other vertebrates^{3,9}. An integrative cross-taxon approach to this phenomenon will likely further our understanding of intraspecific niche use and the evolution

Discrete resource polymorphisms occur in various vertebrate species and probably occur more frequently than is generally appreciated. They are manifested in a number of ways, including morphological,

behavioral and life history characters. Research on a number of unrelated taxa suggests that resource polymorphisms may be underestimated as a diversifying force and potentially play important roles in population divergence and initial steps in speciation. In an ecological context, they are important in resource partitioning and reducing intraspecific competition. Recent research suggests that the mechanisms maintaining these polymorphisms may be similar in diverse taxa, that phenotypic plasticity is

taxa, that phenotypic plasticity is important, and that some are under simple genetic control.

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 San Francisco State University, 1600 Holloway Ave, San Francisco, CA 94132, USA. lap are likely to be the result of ecological pressures experienced in sympatry.

Nature of discrete phenotypic differences

Polymorphisms associated with segregation in habitat and diet show considerable diversity (Table 1, Box 1). Some morphological differences between morphs are so subtle that the discrete nature of the variation is easily overlooked, while others are so dramatic that they were first misidentified as distinct species^{3,10}. Dramatic examples include arctic charr (Salvelinus alpinus), which show as many as four sympatric morphs, normal and cannibalistic morphs of the tiger salamander (Ambystoma tigrinum), larval morphs of the spadefoot toad (Scaphiopus multiplicatus), which differ in size and morphology, and the African finch or seedcracker (Pyrenestes ostrinus) with small and large bill morphs (Fig. 1). All these morphs are as morphologically different, and

of intraspecific variation and speciation. Moreover, studying differentiated morphs can be advantageous in ecological studies, especially those involving competition. Unlike sympatric species, which may have evolved ecological differences in allopatry, discrete morphs have identical phylo-genetic histories; thus, differences in resource overshow differences in feeding ecology and behavior, as distinct congeneric species. Examples of more subtle polymorphisms include two sympatric morphs of the pumpkinseed sunfish (*Lepomis gibbosus*), which are differentiated on the basis of body form and gill raker architecture, with each morph differing with respect to its limnetic or benthic lake habitats and diet^{11,12}. Still another potential class of variation, not discussed in detail here, includes closely related species that are trophically differentiated, but where hybridization and introgression occur frequently¹³.

Resource polymorphisms are not restricted to morphological differences but may also have significant life history and behavioral components associated with differences in food and habitat among morphs. Fish morphs often differ in growth patterns, which are typically related to differences in age at maturity, ontogenetic niche shifts and/or variable migratory behaviors, while amphibian morphs typically differ in growth patterns and size at metamorphosis (Box 1). Studies of oystercatchers (Haematopus ostralegus) reveal two types of individuals in some populations, 'stabbers', which feed on mussels by pushing their bills between the valves of the mussel, and 'hammers', which crack the mussel open by pounding¹⁴. Wear imposed by differences in feeding behavior results in the two bill shapes, pointed and blunt, which can change seasonally.

Ecological context

What are the ecological conditions that promote resource polymorphisms? A growing number of studies suggests that a relaxation of interspecific competition and the availability of open niches are essential. In many young lakes in recently glaciated regions of the northern hemisphere, freshwater fish typically occupy benthic or limnetic habitats^{1,2}. For instance, pumpkinseed and bluegill sunfish (Lepomis macrochirus) cooccur and occupy distinct ecological niches, adult bluegills are generalists, occupying open water and feed on zooplankton, while pumpkinseeds specialize on snails and occur in shallow water.

Robinson *et al.*¹¹ found that where only pumpkinseeds occurred in lakes they had differentiated into two morphs – the typical form, which feeds on snails, and an open-water morph with modified gill arches, which feeds on zooplankton.

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

Species	Nature of discrete ecological differences	PD٥	Refs
Fishes			
Arctic charr (Salvelinus alpinus)	Benthivory, planktivory, piscivory, migration	m,b,l	4,15-17,23
Brook charr (S. fontinalis)	Benthivory, planktivory, swimming activity	m,b	44
Brown trout (Salmo trutta)	Benthivory, planktivory, piscivory, migration	m,b,l	1,40
Sockeye salmon (Oncorhynchus nerka)	Benthivory, planktivory, migration	m,b,l	1,8,24
Lake whitefish (Coregonus clupeaformis)	Benthivory, planktivory, piscivory, migration	m,b,l	1,2,9,32
Scandanavian whitefish (Coregonus spp.)	Benthivory, planktivory, piscivory	m,b,i	1,2,9,32
Rainbow smelt (Osmerus mordax)	Benthivory, planktivory, piscivory, migration	m,b,l	41
Stickleback (Gasterosteus aculeatus)	Benthivory, planktivory	m,b	1,2,9,19,21
Bluegill sunfish (Lepomis macrochirus)	Benthivory, planktivory	m,b	1,9,27
Pumpkinseed sunfish (L. gibbosus)	Benthivory, planktivory	m	1,9,11
Cichlids (Perissodus spp.)	Eating scales from left vs right side of live fish	m	6
Cichlid (Cichlasoma minckleyi)	Feeding on snails and plant material	m,b	1,9,32
Cichlid (C. citrinellum)	Feeding on snails and soft-bodied prey	m,b	1,9
Goodeid fish (Ilyodon spp.)	Strong indication of differences in food	m	1,9
Neotropical fish (Saccodon spp.)	Different techniques in eating algae	m	1
Amphibians			
Spadefoot toad (Scaphiosus multiplicatus)	Omnivory, carnivory, cannibalism	m,l	22,26
Tiger salamander (Ambystoma tigrinum)	Invertebrate diet, cannibalism, different adult habitats	m,l	34
Reptiles			
Soft-shelled turtles (Trionyx spp.)	Insectivory, piscivory, omnivory	m	9
Birds			
African finch (Pyrenestes ostrinus)	Feeding on soft- and hard-seeded sedges	m	5,10
Oystercatchers (Haematopus ostralegus)	Different feeding techniques on mussels	m,b	14
Blackcap warbler (Sylvia atricapilla)	Differences in migratory routes	b	45
Cocos finch (Pinaroloxias inornata)	Food: arthropods, nectar, fruit, seeds, molluscs, lizards	b	18
Hook-billed kite (Chondrohierax unicinatus)	Feeding on different size clams and snails	m	46
Mammais			
Deer mice (Peromyscus maniculatus)	Woodland vs grassland habitats and diets	m,b	9

^aWe define resource polymorphism as the occurrence of discrete intraspecific morphs showing differential niche use, usually through differences in feeding biology and habitat use. Here, we do not specifically discuss cases where resource polymorphism may only affect one sex or polymorphisms that are clearly based on alternative mating strategies. However, such a relationship can be important because, like food and habitat, a mate is obviously a 'resource', and especially, for the purpose of this review, because this interaction has bearing on the evolution of prezygotic isolation mechanisms between resource morphs.

Phenotypic difference, PD; morphological, m; behavioral, b; and life history, I.

Box 1. Some phenotypic differences among morphs of fish, amphibians and birds

Phenotypic differences between morphs vary widely across taxa and whether they are based on morphology, life history traits and/or behavior they tend to be highly correlated with diet and habitat use1.2.4.5.8.9.11.15.16.20.26.

Fish: morphs typically differ in jaw size and jaw shape, and size, shape and number of gill rakers. Other external and internal structures may also be involved, including size and shape of fins, body and head depth, structure of stomach and gut^{1,2,9,11,15,17,19,32,41}. Benthivorus morphs generally have a blunt snout, the lower jaw is shorter than the upper jaw, and they have a less streamlined body than planktivorus and piscivorous morphs, which have a pointed snout and jaws similar in length^{1,2,9,15,32} (Fig. 1). Differences in life history, such as growth pattern, age at maturity, reproductive investment, fecundity and egg size are especially common in morphs of salmonids^{8,15,17,23,24}. Differences are seen in foraging behavior and techniques^{9,16,27,32} and migratory behavior ^{8,15,24}. Discrete differences in foraging and social behavior have also been noticed in young salmonids⁴⁴.

Amphibians: morphs display external and internal differences in trophic structures such as teeth and mouth size and length of intestines^{22,20,34}. Both age and size at metamorphosis may differ^{22,34}. Carnivorous and cannibalistic larval morphs may develop faster, metamorphose earlier and have larger trophic structures than non-cannibalistic morphs (Fig. 1). In some cases, differences in food and trophic morphology occur both in larvae and adults³⁴. Differences are seen in maturation patterns retaining larval phenotype and becoming sexually mature in the larval aquatic habitat or metamorphosing and becoming sexually mature in the typical adult terrestrial habitat^{34,47}.

Birds: differences in trophic morphology primarily involve shape and size of bill^{10,14}. For example, morphs that specialize on hard seeds have wider bills than morphs that specialize on soft seeds. Discontinuous differences may also occur in foraging behavior and technique^{14,18} and migratory behavior⁴⁵.

They hypothesized that the open-water morph occupies the niche left 'empty' by the bluegill sunfish. Similarly, arctic charr are recent invaders to postglacial freshwater systems where interspecific competition for food and habitat is low



Fig. 1. (a) Four morphs of arctic charr (Salvelinus alpinus) from Thingvallavatn in Iceland (all individuals are adults). From top down: large benthivorous charr (33 cm long), small benthivorous charr (8 cm long), piscivorous charr (35 cm long) and planktivorous charr (19 cm long). Photograph by S. Skúlason. (b) Small- and large-billed male morphs of the African finch (Pyrenestes ostrinus). Photograph by T. Smith. (c) Larval morphs of spadefoot toad (Scaphiosus multiplicatus). Photograph by D. Pfennig. (d) Cannibal (top) and typical (bottom) larval morphs of the tiger salamander (Ambystoma tigrinum). Photograph by J. Collins.

or absent promoting the subsequent evolution of different morphs.

Benthivorous, planktivorous and/or piscivorous morphs of arctic charr are found together in a number of lakes¹. In one volcanic lake in Iceland, where interspecific competitors are very few and available resources are unusually distinctive, four morphs display substantial morphological and behavioral specialization, apparently greater than in most other cases of sympatric charr morphs^{4,15–17}. Another example where the occurrence of 'empty niches' and the lack of interspecific competition seems to be operating is in the Cocos finch (Pinaroloxias inornata), endemic to the isolated Cocos Island. Lacking interspecific competitors, the Cocos finch has diversified intraspecifically, and while showing little morphological variation exhibits a stunning array of stable individual feeding behaviors spanning several families of birds¹⁸. Under certain circumstances, resource polymorphisms may also arise in species-rich environments, if particular resources are underused. For example, small- and large-billed morphs of the African finch have evolved in subsaharan Africa, a region known for exhibiting the highest species diversity of granivorous birds. Here, the polymorphism is maintained by morphs specializing on extremely hard sedge seeds, a resource that other species cannot easily $use^{5,10}$.

Mechanisms and processes

Selection

In several studies, frequency-dependent and disruptive selection have been shown to play important roles in the maintenance of trophic polymorphisms. One of the most

stunning examples where frequency-dependent selection appears to maintain a resource polymorphism is in the Lake Tanganyika scaleeating cichlid fish (Perissodus *microlepis*)⁶. The species exhibits a right- and left-handedness in jaw morphology; right-handed morphs remove scales from a prey's left side, while left-handed morphs remove scales from the prey's right side. Hori⁶ showed that ratios of morphs fluctuate around 1:1 and that the genetic polymorphism is maintained by frequency-dependent selection exerted by the prey's alertness to the side of attack. Individuals of the rarer morph are at a selective advantage because the prey anticipates and guards against attacks from the particular side of the more common morph.

In the African finch, billsize polymorphism appears to be maintained, in part, by disruptive selection resulting from differences in feeding performance on important seeds⁵. Morphs feed primarily on seeds of two species of sedge, which differ in hardness. Large-billed morphs

ness. Large-billed morphs feed more efficiently on hard-seeded sedge, while small morphs feed more efficiently on soft-seeded sedge.

In many lakes in British Columbia, Canada, the threespine stickleback (Gasterosteus aculeatus) occurs as highly specialized benthic and limnetic forms that differ in trophic morphology^{2,19}. While it is unclear whether or not these forms represent discrete species or morphs, each form performs relatively better and exhibits a higher fitness in its respective habitat, suggesting that divergent selection has been important in their possible evolution from extant monomorphic populations that show intermediate morphologies^{20,21}. In general, the likely function of divergent selection (e.g. selection against intermediates) in the evolution of sympatric morphs and/or new species of freshwater fish in the northern hemisphere has probably been largely based on intraspecific competition for food between phenotypically similar individuals. Subsequent, increased phenotypic divergence of sympatric forms probably reduces competition between them; this has recently been discussed in the context of character displacement^{1,2}.

In New Mexico, USA, omnivorous and carnivorous larval morphs of the spadefoot toad coexist in ephemeral ponds. Because of faster developmental rates the carnivorous morph is favored in short-duration ponds, but in longer-duration ponds, the slower-developing omnivorous morph is favored because their larger fat reserves enhance post-metamorphic survival. In ponds of intermediate duration, the abundance of each morph is frequency dependent²².

Sympatric morphs can evolve rapidly. In the case of polymorphic freshwater fish in the northern hemisphere, their segregation has taken place in <15000 years following the latest glaciation period². In some of these species, morphs can be formed very quickly, even within one generation, following a single stocking or invasion event, primarily because of discrete environmental influences on growth^{8,17,23,24}. New endemic morphs, and even new species, of cichlid fishes may have evolved in Lake Malawi in 200 years or less²⁵.

Phenotypic plasticity and genetic basis

Phenotypic differences among morphs can result from phenotypic plasticity (Box 2). Morphs of the tiger salamander and the spadefoot toad arise primarily through a

phenotype-mediated response to varying densities of conspecifics and food type^{22,26}. Food type and quality may also change trophic morphologies in several species of cichlid fishes^{7,9} and in the pumpkinseed sunfish¹². Recent studies on polymorphic fish illustrate the varying degrees of plasticity in foraging behavior and technique within and among morphs^{16,27}. Feeding on a particular prey can result in plastic changes in trophic structures, and may lead to greater morph specialization⁹. Furthermore, life history variation is extremely plastic in salmonids and can be linked to flexibility in juvenile behaviors (Box 2)²⁸.

In at least two studies, the genetic basis of trophic polymorphisms appears to be controlled at one locus with two alleles. Bill size polymorphism in the African finch appears to be determined by a single autosomal di-allelic locus with complete dominance for large bill⁵. Similarly, handedness in the scale-eating cichlids also appears to be determined by one-locus with two alleles⁶. The simple genetic control of at least some polymorphisms and implications in others (Box 2) suggests that reaching new adaptive peaks may occur through mutations of large effect²⁹. This and other potential explanations need to be examined. Detailed investigations of the genetic basis of resource polymorphisms are becoming increasingly important (Box 2).

Phenotypic plasticity and underlying genetic variability may interact in shaping polymorphic traits (Box 2)³⁰. For example, while the trophic morphology of the threespine stickleback is largely genetically determined, adaptive plasticity in trophic morphology is also important^{19,31}. In arctic charr phenotypic differences among sympatric morphs are determined both by genetic and environmental factors, and their relative importance apparently differs among cases, and appears to be related to the level of specialization of morphs in different lakes^{16,17,23}.

The developmental basis of polymorphic traits, although important, has been little studied. Size and shape of muscles and bones, for instance, in the trophic apparatus of fish, can be greatly modified by the physical processes of feeding¹². Also, different morphological patterns may arise through allometric growth patterns³². Phenotypic differences among sympatric morphs can result from evolutionary changes [e.g. related to regulatory gene(s)] in the timing of developmental events (heterochrony³³), in some cases as early

Box 2. The role of genetic and environmental factors in generating resource polymorphisms and the importance of behavior

Phenotypic differences between morphs can be determined by genetic and/or environmental effects on development (phenotypic plasticity⁴⁸). Thus, an alternative morph adopted by a particular individual can depend on the environmental condition (internal and/or external to the organism), genetic effects or a combination of both³⁰. Such a switch of a genotype to an alternative behavior, morphology or life history may be based on a threshold for phenotypic expression, which can be reached by continuous underlying distribution of genetic effects and/or continuous responses to environmental stimuli^{3,48,49}. In some cases, switches can have a simple genetic^{5,6} or environmental²⁸ basis. Most studies indicate that alternative morphs are conditional and non-reversible but some morphs may show reversible plastic phenotypes^{7,22}.

Switches based almost exclusively on phenotypic plasticity seem to have evolved in unstable environments^{22,23,34}. Switches under strong genetic control^{5,6} may evolve in relatively stable selective regimes. Environmental and genetic factors may interact positively, for example, together producing relatively greater and/or more-refined phenotypic differences between morphs³¹. Sympatric morphs may experience different selective regimes, for instance, differences in availability or behavior of their preferred prey, and this can result in varying levels of plasticity of these morphs^{16,31}. For example, the more variable diet of the limnetic form of the threespine stickleback, compared to the benthic form, was associated with greater plasticity in trophic morphology in the former than in the latter³¹. If ecological segregation is persistent and morphs become reproductively isolated, a switch producing alternative morphs may become less important or absent³⁰.

Behavioral variation may be a crucial basic feature of resource polymorphism^{9,16,28,30,38}. Behavior is typically more flexible than morphology and behavioral differences are often considered to precede segregation in morphological and life history characters^{28,30}. The following is one possible evolutionary scenario involving behavior. Since different food types can influence morphology and life history in fish, variable choice of food by sympatric morphs may cause differences in morphology, growth and maturity patterns^{7,23}. This process can lead to less behavioral flexibility within morphs, for instance, because changes in trophic morphology and/or life history owing to a particular food can limit feeding efficiency on an alternative prey, possibly resulting in greater ecological specialization of morphs^{9,28}.

as during embryonic development. This developmental timing can be affected both by environmental and genetic factors^{7,17,32,34}. Evolutionary release from developmental and/or functional constraints can greatly increase the possibility for certain groups of animals to exhibit polymorphisms. For example, it has been suggested that such a release of functional constraints in the jaw structures of cichlids greatly diversified their feeding behavior, explaining, in part, their subsequent extensive ecological diversification³⁵.

Population differentiation and speciation

What is the role of resource polymorphisms in speciation? Discrete intraspecific variation is frequently mentioned as the initial step in speciation and has been emphasized in theoretical models of sympatric speciation^{30,36–38,50}. A preeminent early model of sympatric speciation³⁷ showed how a single population using two distinctly different niches could become reproductively isolated. Central to this model is that a stable polymorphism evolves first, with reproductive isolation occurring later by morphs reproducing separately in the two niches. Proposed examples of sympatric speciation usually involve analyses in which the process of sympatric speciation is inferred from the dispersion pattern of already discrete species or races. In this respect, species that show resource polymorphisms present unique opportunities for studying the process of speciation. Bush³⁹ emphasized this aspect in a recent review of sympatric speciation and pointed out that polymorphisms probably play a prominent role in establishing habitat specialization, a necessary prerequisite in most models for reproductive isolation.

In many cases, reduced gene flow between sympatric morphs suggests population divergence and even incipient speciation^{3,8,24,40,41}. This may result from either postzygotic mechanisms, such as reduced fitness of hybrids^{20,24}, or prezygotic mechanisms, such as spatial and temporal segregation in breeding (often greatly promoted by philopatry) and differences in breeding behavior or mate choice^{17,32,42}. Such isolating mechanisms can easily co-evolve with the phenotypic attributes, such as size and color, and the ecological segregation that characterize the different adaptations of morphs in their respective niches^{11,17,25,32,42}. Within and among species of freshwater fish, population segregation has repeatedly occurred within the same freshwater system and even within the same lake^{3,8,41} and the degree of the genetic divergence between sympatric morphs is highly variable. In some cases, gene flow is almost unimpeded, while in others, sympatric morphs may appear partially or completely reproductively isolated^{3,40}.

A recent review by Rice and Hostert⁴³ suggests that nichespecific adaptation, typical of resource polymorphisms, is a key element in divergence and speciation. In their divergencewith-gene-flow model, they believe that speciation is likely to occur under a range of conditions lying along a continuum. Towards the middle of this continuum are populations making up a geographic gradient (or cline) with opposing phenotypes favored at each end. 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 with traits important in resource use. Rice and Hostert⁴³ refer to this as reproductive isolation via pleiotropy and/or genetic hitchhiking. Under this model, discrete resource polymorphisms could represent important early building blocks in the speciation process, via the following steps: (1) invasion or exploitation of either novel or unexploited resource - filling 'open' niches; (2) a decrease in intraspecific competition; (3) multifarious selection in each niche leading to the evolution of a polymorphism, or adaptation via mutation of large effect, resulting in morphs occupying new adaptive peak(s); (4) reduced gene flow and the evolution of prezygotic reproductive isolation as a correlated character (pleiotropy and/or genetic hitchhiking). If this model of speciation is shown to be a dominant one, as laboratory experiments seem to suggest, could it provide a simple explanation for why resource polymorphisms are not more common in natural populations? Is it because discontinuous variation of this kind more often leads to reproductive isolation and speciation than stable polymorphisms?

Conclusions and perspectives

It is intriguing that resource polymorphisms have been generally underestimated as a diversifying force. Perhaps this is because of the misconception that adaptive evolution should always give rise to unimodal entities³⁸. Implicit in the various examples discussed here is the notion that alternative adaptive phenotypes are probably more common and evolutionarily important than presently recognized³⁸. The presence of resource polymorphism in the bluegill and pumpkinseed sunfish was only recently discovered despite many decades of ecological and behavioral work on these species. Searching for more cases across vertebrate taxa by looking for subtle differences is likely to be fruitful, especially in groups such as birds and mammals. The interactions among phenotypic plasticity, development, genetics and selection, their role in adaptive radiations (as seen in African cichlids^{25,32}), and why resource polymorphisms appear more common in some taxa than others, are important areas of future investigation.

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