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ECOLOGICAL CAUSES OF ADAPTIVE RADIATION

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Abstract.—According to the naturalists of the first half of this century, adaptive radiation is the outcome of three ecological processes: phenotypic differentiation of populations by resource-based divergent natural selection, phenotypic differentiation through resource competition (ecological opportunity and divergent character displacement), and ecological speciation (speciation as a consequence of adaptation to different resource environments). Despite a recent surge of interest in the phenomenon, especially in phylogenetic histories of radiations, we know too little about the ecology of most radiations to assess the roles of the three processes. I summarize our own efforts to test the theory with a radiation of three-spined sticklebacks apparently still in its early stages. The role of divergent selection is supported by a strong relationship among populations and species in mean morphology, feeding performance, habitat use, and growth rate. Trade-offs in feeding performance and growth rate between habitats are steep. Ecological character displacement is indicated by the large differences between sympatric species and the intermediate features of solitary species inhabiting lakes of similar size. A pond experiment showed that natural selection on a solitary species is altered following introduction of a competitor and favors divergence. Evidence for ecological speciation in sticklebacks is weakest, but there are several hints of its importance: speciation was rapid and accompanied by divergence into different ecological niches; selection against hybrids is stronger in the wild than in the laboratory, which suggests that hybrid fitness depends on ecological context; premating isolation depends in part on traits that diverged in association with the exploitation of different resources; and reproductive isolation may have evolved in parallel in different populations experiencing similar environmental conditions. Comparison with other studies suggests that these findings apply broadly.

Adaptive radiation is the diversification of a lineage into species that exploit a variety of different resource types and that differ in the morphological or physiological traits used to exploit those resources (Huxley 1942; Futuyma 1986). It involves both the formation of species and the evolution of ecological differences between them. Many cases of adaptive radiation have been suggested, but the most extraordinary are those marked by youth, an unusual degree of differentiation in resource use, large differences in trophic morphology, and a high degree of sympatry among descendant forms. These include the Galápagos finches (fig. 1) (Lack 1947; Bowman 1961; Grant 1986); the Hawaiian honeycreepers (Amadon 1950); various Asteraceae of Hawaii including silverswords (Carr and Kyhos 1981; Baldwin et al. 1991), *Bidens* (Helenurm and Ganders 1985), and *Tetramolopium* (Lowrey 1995); the Hawaiian *Drosophila* (Carson and Kaneshiro 1976); and cichlids of East African lakes (Fryer and Iles 1972; Greenwood 1981; Meyer 1993).

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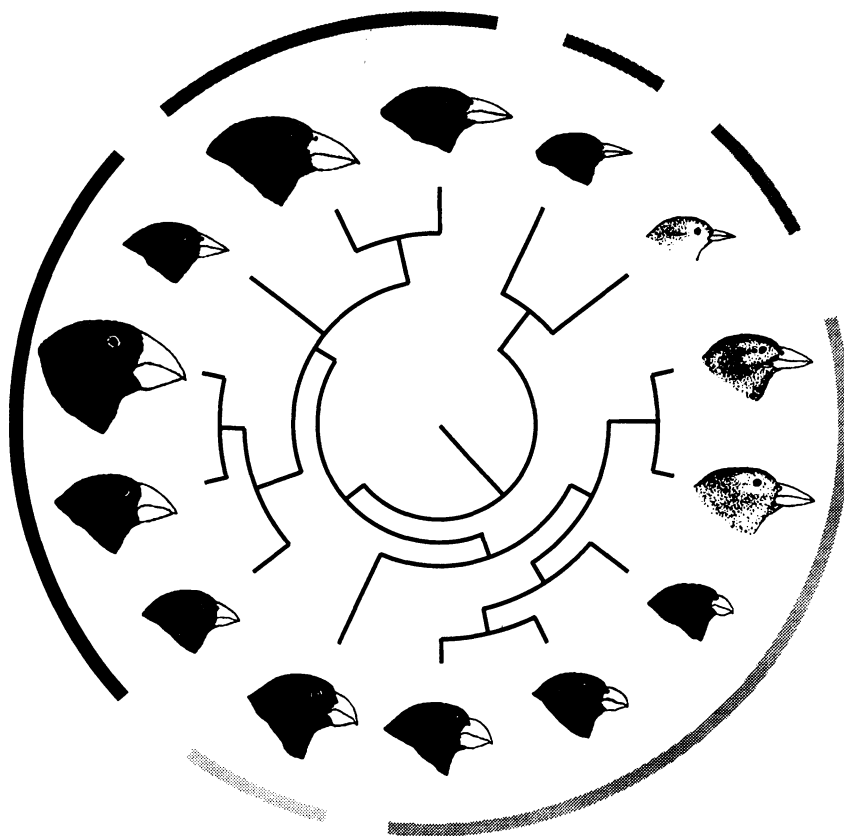


FIG. 1.—Heliogram for the adaptive radiation in Darwin's finches. Shading of the peripheral wheel identifies different dietary groups, beginning with the darkest and moving clockwise: ground finches (*Geospiza*), cactus finches (*Geospiza*), Cocos finch (*Pinaroloxias*), warbler finch (*Certhidea*), tree finches (*Camarhynchus*), and vegetarian finch (*Platyspiza*). Phylogenetic relations are those according to Lack (1947) and are similar to those based on electrophoresis of a large subset of the species (Yang and Patton 1981). (Modified from Grant 1986 after Swarth 1931 and Bowman 1961.)

In this article I consider the ecological causes of adaptive radiation. I begin with a brief review of the basic theory concerning the ecological processes that take place during diversification. This theory represents the collected views of many naturalists writing before about 1950. It was widely accepted then and has guided field studies of adaptive radiation ever since. Yet, the major elements of this ecological theory have rarely been tested—never in their entirety in any single radiation. Second, I summarize our own efforts to test elements of this theory with a recently discovered radiation of three-spined sticklebacks (*Gasterosteus* sp.) that inhabit small lakes and nearby marine waters of coastal British Columbia, Canada. The system is ideal for study because of its recency, its simplicity, the apparent independent replication of evolutionary events on a small

geographical scale, the presence of spatial variation in interspecific interactions—especially competition and possibly hybridization—and the feasibility of experimental manipulations.

ECOLOGICAL THEORY OF ADAPTIVE RADIATION

I employ the traditional definition of adaptive radiation: a proliferation of species within a single clade accompanied by significant interspecific divergence in the kinds of resources exploited and in the morphological and physiological traits used to exploit those resources (Huxley 1942; Lack 1947; Mayr 1963; Carlquist 1974; Futuyma 1986; Grant 1986). This definition does not include the proviso that adaptive significance of species differences must be rigorously established, mainly because the criteria for adaptation are themselves problematic (Endler 1986; Baum and Larson 1991; Harvey and Pagel 1991; Lauder et al. 1993). The role of adaptation is considered instead when testing ecological theories of the causes of speciation and ecological, morphological, and physiological differentiation (i.e., adaptive radiation).

According to the naturalists writing before 1950, divergent natural selection is the ultimate cause of adaptive radiation. Three processes were thought to be involved (Fisher 1930; Dobzhansky 1937; Huxley 1942; Mayr 1942; Simpson 1944, 1953; Lack 1947). The first is differentiation of populations and species in phenotype (morphology and physiology) caused by differences in the resource environments they experience. The idea is that each set of available resources subjects its consumer species to distinct selection pressures, owing to the advantages of specific combinations of traits for efficient resource exploitation. By “resources” I mean utilizable features of environment including food (and access to food) and enemy-free space (Jeffries and Lawton 1984).

The second process is phenotypic differentiation caused by competition for resources (divergent character displacement). Competition between closely related species was thought to drive their divergence onto new resource types, where they would become subject to different selection pressures. This process is just a special case of the first, in that each species is presumed to alter the resource environment in such a way that natural selection pressures acting on other species are changed. However, separate consideration is warranted here because the importance of competition in divergence has been so controversial. Also, character displacement between related species applies only to the sympatric subset. The other side of the competition hypothesis is “ecological opportunity,” which may be loosely defined as a wealth of evolutionarily accessible resources underutilized by species in other taxa (Simpson 1944, 1953). Ecological opportunities arise when new or previously inaccessible resources are either fortuitously encountered (e.g., on a remote archipelago or in a newly formed lake) or are newly exploitable following the acquisition of a morphological or physiological novelty (“key mutation” or “key evolutionary innovation”) (Simpson 1944, 1953; see Heard and Hauser 1994).

The final process is ecological speciation. By *species* I mean the biological concept (“groups of actually or potentially interbreeding natural populations

which are reproductively isolated from other such groups"; Mayr 1942, p. 120) modified to accommodate possibly imperfect reproductive isolation between good species. Ecological speciation is the evolution of reproductive isolation as a consequence of resource-based divergent natural selection and resource competition. I use the term *ecological* to group under a single hypothesis several modes of speciation that involve a common class of adaptive mechanisms, whether the process occurs in sympatry or allopatry, and whether or not natural selection acts directly on reproductive isolation. Under this hypothesis speciation in adaptive radiation results from the same processes that drive phenotypic and ecological differentiation. The by-product (indirect) mechanism was seen by the early naturalists as the most likely route to ecological speciation: pre- and postmating isolation arise incidentally as populations accumulate genetic differences favored in different resource environments (Fisher 1930; Dobzhansky 1937; Mayr 1942). A second route was reinforcement, whereby partial postmating isolation arising from environmental selection pressures directly favors the evolution of premating isolation (Fisher 1930; Dobzhansky 1937).

Researchers then and now realized that mechanisms other than divergent selection can also cause speciation. For example, Lack (1947) believed that nonadaptive processes were the major factor in speciation of the Galápagos finches. Non-ecological modes of speciation include genetic drift in stable populations (Wright 1940) (including divergence in sexual preferences; Fisher 1930; Lande 1981), drift through founder events and population bottlenecks (Mayr 1954), and fixation of alternative advantageous genes in allopatric populations experiencing identical selection pressures (Muller 1940). There is no doubt that given enough time speciation will occur via one of these alternative mechanisms in the absence of significant ecological differentiation of populations. However, the main question of interest here is whether speciation during adaptive radiations involves resource-based natural selection and competition instead, especially when it occurs rapidly. I therefore focus on the possibility of ecological speciation here rather than on other classes of mechanism.

None of these three processes of adaptive radiation is well understood. The idea that phenotypic differentiation is caused by divergent selection between resource environments is perhaps uncontroversial, but direct documentation is surprisingly scarce. Differences between environments in the form and intensity of selection have rarely been quantified. The role of interspecific competition on ecological and morphological diversification is more contentious, and few convincing examples exist. The extent to which natural selection pressures on a species are altered by the presence in the same environment of a competitor is simply unknown. (The effects of other interspecific interactions on diversification, especially predation and parasitism, are even less well understood than competition.) Finally, little is known about the role of ecological selection pressures in speciation. Unequivocal examples of ecological speciation in the wild are few because other mechanisms of speciation are difficult to rule out. Field studies of natural selection on reproductive isolation are in their infancy.

The work described here investigates these three ecological processes in diversification of sticklebacks: differentiation through resource-based divergent selec-

tion, differentiation through competition, and ecological speciation. The study is not complete, and many findings are tentative. Nevertheless, the results are sufficiently informative to allow the drawing of some conclusions about the role of ecology in this adaptive radiation.

ADAPTIVE RADIATION IN STICKLEBACKS

The three-spined stickleback (*Gasterosteus aculeatus*) is a holarctic marine planktivorous fish that spawns in the lower sections of coastal rivers and streams (Bell and Foster 1994). The species has independently given rise to a large number of permanent freshwater populations throughout its range (Bell and Foster 1994; Ortí et al. 1994). At least some of these freshwater descendants are reproductively isolated from the marine (anadromous) species (Hay and McPhail 1975; Borland 1986; Zuiganov et al. 1987). Our work focuses on a subset of these—the sympatric species pairs of sticklebacks that occur in several small coastal lakes in the Strait of Georgia region of British Columbia, Canada (McPhail 1984, 1992, 1994; Schluter and McPhail 1992).

Species pairs occur in four unconnected drainages on three adjacent land masses in the Strait of Georgia: Vancouver Island (Enos Lake), Texada Island (Paxton Lake and Priest and Emily Lakes), and Lasqueti Island (Hadley Lake, where both species have recently become extinct). Most comparable lakes in the same region contain only a single species. In every case, one species (the limnetic) is smaller and has a more slender body, a narrower mouth, and longer, more numerous gill rakers than the second species (the benthic). (Rakers are protuberances along the gill arches that aid in the retention of ingested prey, acting as a physical sieve and, when very densely packed, directing water currents within the buccal cavity; Sanderson et al. 1991.) These morphological differences are associated with distinct habitat preferences and diets: limnetics are mainly planktivorous and forage offshore in the water column, especially in the nonbreeding season, whereas benthics are confined to the littoral zone and deeper areas of open sediment where they consume invertebrates living on or in the sediments or attached to vegetation (Larson 1976; Bentzen and McPhail 1984; Schluter and McPhail 1992; Schluter 1993). During breeding, males of both species build nests and defend territories in the littoral zone.

Sympatric sticklebacks are biological species rather than morphs of a single species. Most phenotypic differences are heritable (McPhail 1984, 1992) and probably polygenic (Hatfield 1995), although differences in some traits are exaggerated during development by diet (Day et al. 1994). The species mate assortatively in the laboratory (Ridgway and McPhail 1984; Nagel 1994; Hatfield 1995), and wild F_1 hybrids (identified by their intermediate morphology) are rare (McPhail 1984, 1992). Nevertheless, the species are very young: sympatric forms differ in allele frequencies at only two or three of 25 allozyme loci screened (Nei's [1978] $D \approx 0.02$; McPhail 1984, 1992). Mitochondrial DNA differences between sympatric species are also slight: nucleotide divergence (a composite index of difference in nucleotide sequence and haplotype frequency; Nei and Miller 1990) between

sympatric limnetics and benthics range from 0.01% in Enos Lake to 0.1% in Priest Lake (Taylor et al. 1996).

The small lakes in which species pairs occur are less than 13,000 yr old, which puts an upper bound on the duration of sympatry (Schluter and McPhail 1992; McPhail 1993). The entire area was glaciated until the very end of the Pleistocene, and the lakes were formed when submerged land rebounded following the removal of ice. Colonization occurred from the sea, probably shortly after the lakes formed, when they were close to sea level. The lakes are presently inaccessible from the sea because of small waterfall barriers. Two geographical models of species origins are consistent with the present distribution of sympatric pairs (Schluter and McPhail 1992). The first is sympatric speciation within lakes. The second model is double invasion, whereby lakes were colonized either in two separate invasions by the same marine ancestor at different dates (Schluter and McPhail 1992; McPhail 1993) or from two sources, one marine and the other freshwater (itself the result of an older colonization by the marine form).

Present evidence on species origins is contradictory. Allozyme data (McPhail 1984, 1992; Withler and McPhail 1985) support the double-invasion model: limnetics in both Enos and Paxton Lakes are more similar to the marine form in allele frequencies than are benthics. Limnetics from Paxton and Priest Lakes are also more similar in salinity tolerance to the marine form than are benthics from the same lakes (Kassen et al. 1995). The geological history of the Strait of Georgia and the close proximity of independent two-species lakes are also more consistent with double invasion than with sympatric speciation (Schluter and McPhail 1992). However, a recent phylogeny based on mtDNA restriction sites is consistent instead with sympatric speciation (Taylor et al. 1996). Limnetics and benthics in each lake are extremely similar to one another and share haplotypes not found in other lakes or in the marine species. There was no tendency for limnetics to be more similar to the marine species than benthics. Further molecular work may reconcile the contradiction between mtDNA and other evidence. Possibly, the allozyme and salinity tolerance measurements are distorted by natural selection. Alternatively, the molecular phylogeny might mislead if hybridization has led to a transfer of mitochondria between sympatric species, obscuring their origins (Taylor et al. 1996).

Although species diversity is still low, the sticklebacks represent an adaptive radiation in the classic sense: speciation has been rapid and is coupled with a large degree of ecological and functionally significant morphological differentiation. Degree of sympatry may appear meager next to, say, the cichlid species flocks of East African lakes, but this simplicity is one of the great advantages of the system for ecological study. Any ecological theory to explain adaptive radiation in general should also apply to these stickleback forms; hence, they serve as a tractable model for testing this theory.

RESOURCES AND DIVERGENT NATURAL SELECTION

Divergent natural selection for efficient exploitation of alternative resources is held to be a fundamental cause of phenotypic differentiation in adaptive radiation.

A strong and feasible test of this theory might consist of two parts: first, a direct measurement and comparison of natural selection pressures on traits in the different resource environments exploited by separate species or semispecies; second, a demonstration that differences in feeding performance (or other index of successful resource exploitation) are responsible for the differences in selection recorded. This test has rarely been applied. Cases include comparisons of selection pressures in single populations of Darwin's finches in the face of fluctuating food environments (Boag and Grant 1981; Price et al. 1984; Gibbs and Grant 1987; Grant and Grant 1989) and disruptive selection on beak size in between morphs of an African finch specializing on different seed sizes (Smith 1993). Estimates of adaptive landscapes for beak size in the granivorous Galápagos finches (Schluter and Grant 1984) and for beak size/shape in the red crossbills of North America (Benkman 1983) also indicate that discrete sets of seed resources favor different beak sizes and that intermediate beaks have relatively low fitness.

I carried out a coarse version of this test that determined whether the present-day morphological differences between limnetic and benthic species render them differently capable of exploiting littoral and open-water habitats. If morphological differences between limnetics and benthics were created by distinct selection pressures in the two environments, then relatively high fitness in one habitat should have come at the expense of reduced relative fitness in the other habitat. In other words, there should be a clear trade-off. This prediction was tested using a transplant experiment in two parts. In the first part, foraging success was measured in individuals of the two species from Paxton Lake (and their hybrids) placed in large aquaria containing either a layer of sediment from the littoral zone or clear open water containing plankton at ambient densities (Schluter 1993). In the second part growth was measured in individuals transplanted between habitats of Paxton Lake in field enclosures. Growth rate was used as a surrogate component of fitness.

The growth trade-off between habitats was very steep (fig. 2), with each species growing at about twice the rate of the other in its preferred habitat (the relevance of the hybrid value will be discussed later; see Ecological Speciation). The statistical significance of the trade-off is confirmed by the large species \times habitat interaction term in an ANOVA of growth rate (Schluter 1995a). This pattern of growth closely matched measured differences between forms in feeding rate, which suggests that growth is determined mainly by foraging success. The trade-off was not simply a consequence of body size (mass) differences between the species, implying that shape differences are also responsible. This conclusion is bolstered by the observation that the species use very different locomotory and feeding modes in the two habitats. Offshore plankton are obtained during steady swimming using pectoral fins or, when calanoid copepods are the main prey, by lunges preceded by a lateral folding of the body into a double bend (S starts; Webb 1976). In contrast, fish foraging in the littoral zone hover close to the bottom where they examine and periodically engulf a mouthful of the sediment. Sediment is rapidly expelled, and prey are retained in the mouth or reingested. Each species adopts the foraging mode of the other when in the latter's preferred habitat but does not achieve the same success even after hours of training (Schluter 1993).

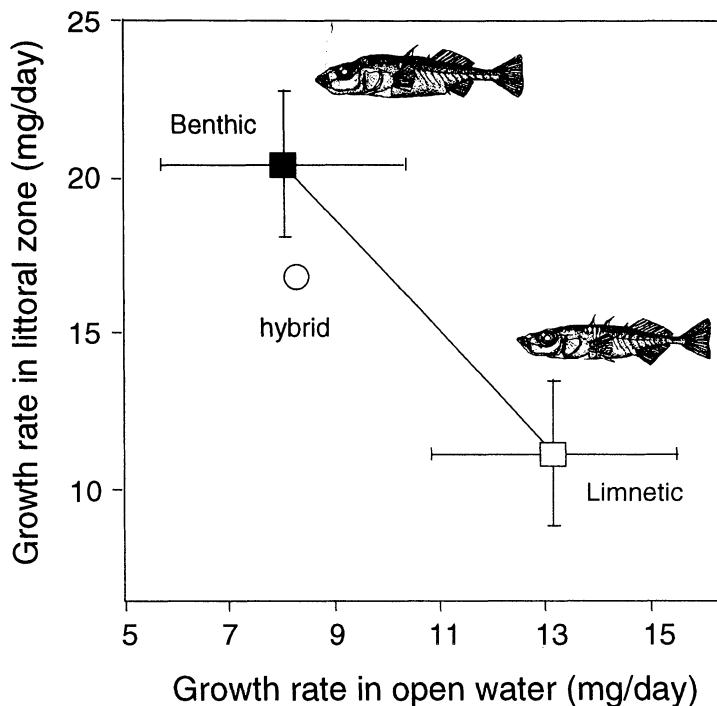


FIG. 2.—Mean growth rates (\pm SE) of limnetics, benthics, and their hybrids in the two main habitats of Paxton Lake. Means are of single individuals placed in enclosures in the two habitats for a 3-wk period (Schluter 1995a). Data from 2 yr were combined after subtracting the average difference between years from the growth measurements. Hybrids were obtained from a wild population established 10 generations previously by the release of F₁ hybrids. A negative slope to the line connecting benthic and limnetic means indicates a trade-off in growth between habitats. The mean for hybrids falls inside this line (toward the origin), which suggests that its growth would be less than the average of the two species if all individuals of the three types chose habitats randomly (i.e., exhibited no habitat preference). (Modified from Schluter 1995a.)

Prey capture success (volume of prey ingested per strike) in littoral sediments was over five times higher in benthics than in limnetics, primarily because they ingested larger prey. Conversely, in open water limnetics achieved a capture success rate three times that of benthics, mainly because of their superior rates of seizure and retention of small prey items.

These trade-offs imply that efficiency of resource exploitation cannot be simultaneously maximized in both littoral and open-water environments and hence that selection is diversifying. A potential criticism of this conclusion is that distinct species do not provide a suitable test of trade-offs because each has been subjected for a long time to only one of the two environments, which has allowed traits with adverse effects in the alternative environment to accumulate incidentally (Futuyma and Moreno 1988; Robinson et al. 1996). If so, then a third morph might exist that combines the best features of the limnetic and benthic species

without compromising foraging success in either of the two habitats. This possibility is unlikely. First, foraging success and growth rate in the different habitats are correlated with alternative combinations of the same morphological traits, and for plausible functional reasons. For example, capture of large prey by benthics in the littoral zone is permitted by their wider mouths; conversely, the small mouth of the limnetic may improve capture of open-water plankton, especially if suction is used (Werner 1977). However, the specific contributions of each morphological trait to foraging success in the alternate habitats is not yet known. Second, similar trade-offs across the same two habitats have been detected among phenotypes within a single population of sunfish, and they involve associations with similar morphological traits (Robinson et al. 1996). Third, stickleback populations occurring alone in small lakes are morphologically intermediate between limnetics and benthics and tend to exploit both habitats (Schluter and McPhail 1992). However, this "third morph" is eliminated when a second species occurs in the lake, probably through character displacement, which implies that intermediate forms are not as successful in the two environments as the two specialists combined. Evidence for such character displacement is discussed next.

DIVERGENT CHARACTER DISPLACEMENT

Evidence for competition's role in adaptive radiation has traditionally come in three forms: exaggerated rates of speciation, morphological evolution, and ecological differentiation in novel or low-diversity environments such as remote archipelagoes, newly formed lakes, or those following mass extinctions (Huxley 1942; Lack 1947; Amadon 1950; Simpson 1953; Grant 1986; Benton 1987; Schluter 1988; Jablonski 1989; Stanley 1989); greater ecological and morphological differentiation between closely related species in sympatry than in allopatry (reviewed in Arthur 1987; Taper and Case 1992); and nonrandom spacing of mean phenotypes in coexisting sets of closely related species (reviewed in Gotelli and Graves 1996). Only a few convincing cases of character displacement are known, which is disturbing in light of its presumed importance in diversification (however, a large number of suggestive cases are known in fish that have not been studied in detail; Schluter and McPhail 1993; Robinson and Wilson 1994). A possible interpretation is that competition's importance has been overblown (Strong et al. 1984; Vrba 1992). Alternatively, character displacement may be difficult to demonstrate because all the evidence is indirect, much of it is unreplicated, and many criteria must be satisfied before alternative interpretations are confidently rejected (Schluter and McPhail 1992, 1993; Robinson and Wilson 1994).

Character displacement in the sticklebacks was initially indicated by observations that species occurring alone in small lakes are morphologically intermediate between paired species (limnetics and benthics) (fig. 3). This pattern is replicated over several lakes and therefore cannot be attributed to chance (Schluter and McPhail 1992). Moreover, morphological differences between the three forms were found to closely predict resource use: solitary species are intermediate between limnetics and benthics in habitat and diet. Different individuals within one solitary population studied in detail (Cranby Lake on Texada Island) primar-

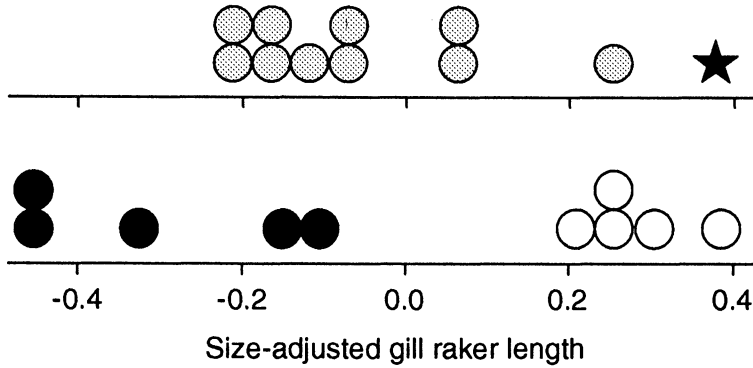


FIG. 3.—Mean morphology in sympatric (*lower*) and allopatric (*upper*) populations of three-spined sticklebacks inhabiting small lakes of coastal British Columbia. Circles are means for benthics (*filled*), limnetics (*open*), and solitary populations (*shaded*). The star indicates the marine species, the probable ancestor of all freshwater populations. (After Schluter and McPhail 1993, from data in Schluter and McPhail 1992.)

ily exploit one habitat or the other according to phenotype, with more limnetic-like individuals taking plankton and more benthic-like individuals exploiting littoral prey (Schluter and McPhail 1992). These comparative data are compelling but indirect and reveal little about the form of the interaction or the strength of divergent natural selection between species. I therefore carried out an experiment to gain insights into the processes of interspecific competition and natural selection and, in addition, to test more directly the hypothesis of divergent character displacement.

The experiment was carried out in two 23 × 23 × 3 m experimental ponds (Schluter 1994). (Pond conditions were as natural as possible. Ponds were previously seeded with plants and invertebrates from Paxton Lake, Texada Island, and all prey species in the diets of experimental fish were the same as those in the wild. Growth rates of experimental fish were similar to those in the wild.) Each pond was split down the middle with a plastic sheet, and a similar number of individuals from a solitary population intermediate in morphology and habitat use (from Cranby Lake, Texada Island) was added to both sides. A planktivore (the limnetic from Paxton Lake) was then added to one side of each pond. The combination of an intermediate form and a planktivore duplicated the presumed ancestral species pair under the double-invasion hypothesis (Schluter and McPhail 1992). The prediction was that, all else being equal, individuals in the Cranby (target) population most similar morphologically and ecologically to the limnetic competitor would suffer disproportionately in its presence, generating natural selection toward a more benthic lifestyle. The experiment was run for 3 mo (i.e., this was a within-generation experiment): young fish were introduced to the ponds in spring and retrieved in late summer, 3 mo later.

This design held density of the target species constant between treatments, such that addition of limnetics to one side also increased total fish density there by 67% (Schluter 1994). The experiment may be criticized for this reason (Ber-

nardo et al. 1995), but controlling for density by topping up the number of fish on the control side is ill advised for a very simple reason: testing whether another species (or morph) alters natural selection on a target requires that only the presence/absence of the second form is varied and that everything else is held constant—especially the density of the target (Schluter 1995*b*). To do otherwise would leave open the possibility that the second species was not the cause of any treatment effect. This is a classic issue in properly designing experiments to test interspecific competition (e.g., Werner and Hall 1977) or any other interspecific interaction. Additionally, without the benefit of hindsight, density variation by itself (i.e., regardless of the morphology and diet of added fish) does not predict that the most planktivorous phenotypes in the target should suffer disproportionately. Consequently, the experiment permitted a strong test of the character displacement hypothesis (Schluter 1994).

To improve the power of the test, levels of phenotypic variation in the Cranby population were increased by hybridizing it to two other species (the limnetic and benthic from Paxton Lake) before introduction. Equal numbers of offspring from three types of crosses were mixed (Cranby \times Cranby, Cranby \times benthic, and Cranby \times limnetic) to create a sensitive experimental “probe” of natural selection pressures over a broad range of phenotypes. This manipulation is similar in principle to direct adjustments of clutch size, tail length, and body size in studies of natural and sexual selection (Roff 1992; Stearns 1992; Andersson 1994) except that hybridization genetically varies the suite of traits. A second reason for hybridizing was to mark different phenotypes by physical features not susceptible to diet-induced phenotypic plasticity (Schluter 1994). Adverse effects of hybridization per se are potentially a concern, but the approach was justified for three reasons. First, no intrinsic reductions in viability or fertility of F_1 hybrids have been detected in any cross to date involving populations in the Georgia Strait (McPhail 1984, 1992; Hatfield 1995; J. D. McPhail, personal communication). Second, any effects of hybridization independent of treatment are controlled for. Third, if hybrids are particularly sensitive to competition regardless of the morphology of the competitor, then both hybrid types (Cranby \times benthic and Cranby \times limnetic) should be equally affected by addition of the limnetic.

The prediction from the hypothesis of character displacement was upheld (fig. 4). In both ponds, growth rate was most reduced in Cranby individuals most similar in morphology and diet to the added competitor. This effect did not appear to be confined to any one cross type within the Cranby hybrid mixture but rather diminished gradually with increasing morphological distance from the limnetic (Schluter 1994). There was no consistent effect on survival of Cranby phenotypes.

These results could be viewed as provisional because they are based on only two ponds, which makes statistical tests of experimental effects problematic (Murtaugh 1995). Nevertheless, the differences in selection are large, consistent, and in the predicted direction. Overall, slopes were significantly different between treatment and control sides (see Schluter 1995*b* for a summary of tests). A paired *t*-test of treatment effect based on the four linear growth differentials is not significant ($P = .11$; the original test result was erroneously reported; Murtaugh 1995), although similar alternatives, such as a paired *t*-test on the *z*-transformed

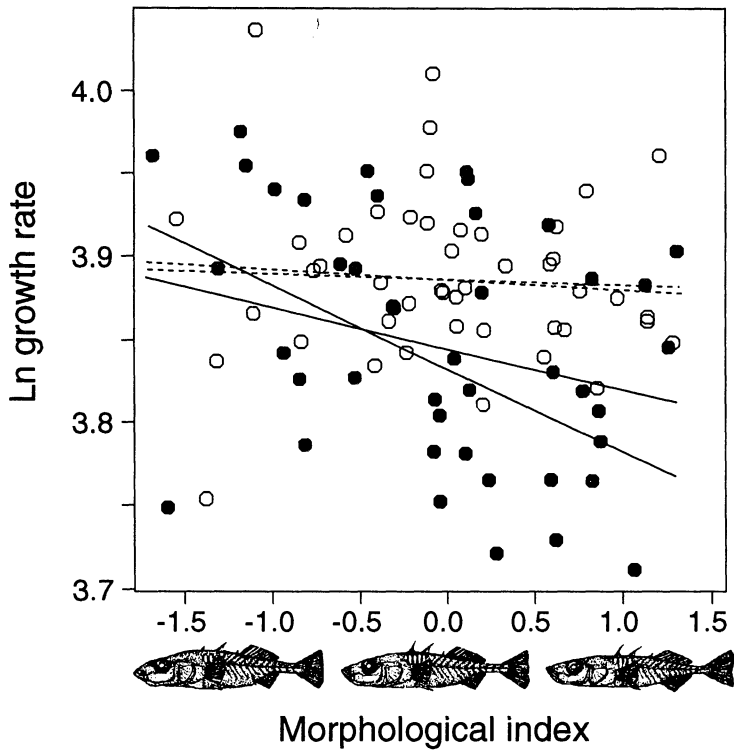


FIG. 4.—Results of the character displacement experiment in two divided ponds. Symbols indicate growth rates of Cranby phenotypes in the presence (*filled*) and absence (*open*) of the limnetic competitor; data are pooled observations from both ponds. Growth differentials (*lines*) are regressions of $\ln(\text{growth rate})$ on morphology in the two ponds separately, in the presence (*solid*) and absence (*dashed*) of the limnetics. The morphological axis distinguishes more benthic-like individuals on the left from more limnetic-like individuals on the right, in arbitrary units. For clarity, each symbol is an average of three adjacent points. (Modified from Schluter 1994.)

rank correlations, are significant. Applying the method of independent contrasts to differences between sides and between ponds reveals that the slope of growth differential is correlated with treatment effect, a result that is robust to assumptions about the magnitude of variance between ponds (see Schluter 1995*b*). The generality of these findings awaits further experimentation, especially in other systems.

It is also useful to ask, ad hoc, whether mechanisms other than character displacement may explain these findings. One possible alternative is density-dependent selection (Bernardo et al. 1995), although I consider this unlikely; that is, it is not easy to come up with a reasonable mechanism whereby only the number of fish, irrespective of their phenotype and diet, generates the pattern in figure 4 (Schluter 1995*b*). Another is that direct aggression, rather than resource depletion, is the mechanism underlying the effect (this is possible but also unlikely

because limnetics are nonaggressive and aggregate in huge schools in the wild when foraging for plankton). A reasonable approach to these concerns would be to repeat the experiment with additional controls for these and other possible factors. However, direct tests of additional predictions of the character displacement hypothesis is perhaps a more fruitful avenue.

Interestingly, if fitness is proportional to growth rate, then even the lesser of the two growth differentials (fig. 4) is sufficient to generate the morphological differences between the modern limnetic and benthic species within 500 yr (Schluter 1994). This calculation is simplistic because it assumes that additive genetic variance in morphology remains constant in time and that selection does not diminish with increasing morphological separation between sympatric species. Though simplistic, the calculation is useful in showing that the duration of sympatry ($\leq 12,000$ yr) is sufficiently long for differences between limnetics and benthics to have evolved by character displacement.

ECOLOGICAL SPECIATION

The final question I address is whether speciation—the evolution of reproductive isolation—during adaptive radiation is driven by the same ecological forces that favor morphological differentiation (i.e., resource-based divergent natural selection and resource competition). My tentative conclusion from the sticklebacks is yes, based on four lines of evidence summarized here, all incomplete. I avoid the issue here of whether speciation occurred in sympatry or allopatry, because we do not yet know. However, ecological speciation is a hypothesis about mechanisms of selection rather than about geographical arrangement of populations per se; therefore, it can be addressed independently. Nevertheless, the mechanism and strength of selection affect the likelihood of sympatric versus allopatric speciation (Felsenstein 1981; Diehl and Bush 1989; Rice and Hostert 1994).

Speciation Is Associated with Ecological Differentiation of Populations and Not Simply with Time

For example, the Pacific Ocean contains two relatively old lineages of *Gasterosteus aculeatus*, whose distributions suggest they derive from a Pleistocene vicariance event (fig. 5). One is found mainly from Japan to Alaska, and the other occurs from British Columbia to California (Haglund et al. 1992; Ortí et al. 1994). Mitochondrial DNA sequence divergence between these lineages is about 2.5%, with the majority of nucleotide differences (83%) occurring at silent sites. The estimated date of the split between the two lineages is about 1 million yr ago, in the mid-Pleistocene (Ortí et al. 1994). Yet, there is little indication that the two lineages represent separate species or maintained much reproductive isolation following secondary contact at the end of the Ice Age. Haplotypes from both lineages coexist within populations where the distributions of the two lineages now overlap, such as in several freshwater populations on the Queen Charlotte Islands (O'Reilly et al. 1993) and northern Vancouver Island (Thompson 1995).

In contrast, the two species in Paxton Lake are indistinguishable in their

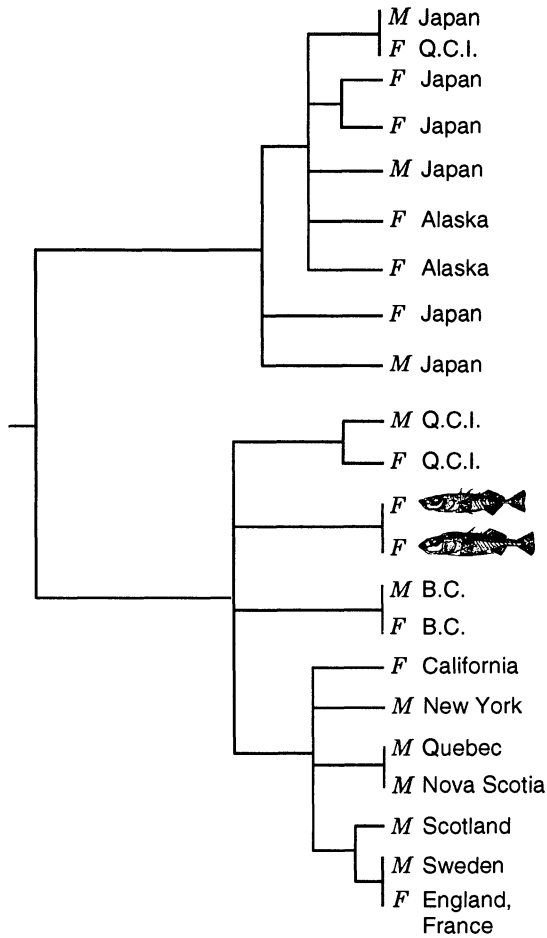


FIG. 5.—Global phylogeny of three-spined sticklebacks according to Ortí et al. (1994). The phylogeny is based on sequences of 747 base pairs in the mitochondrial cytochrome-*b* gene. Branch lengths are roughly proportional to the number of base-pair changes. Note that two old lineages have arisen in the Pacific; these show a sequence divergence of about 2.5%. Atlantic populations are nested within the eastern Pacific lineage. Here *M* refers to marine populations; *F*, to freshwater resident populations; *Q.C.I.*, to populations on the Queen Charlotte Islands, British Columbia. This drawing modifies the phylogeny in Ortí et al. (1994) by replacing the Paxton Lake sample with the two species, which show no differences in the 400-base-pair segment at the 5' end of the same gene (A. Meyer, personal communication) and which are virtually indistinguishable in their frequencies of mtDNA haplotypes (Taylor et al. 1996).

mtDNA sequences (fig. 5) and haplotype frequencies (Taylor et al. 1996), which suggests that reproductive isolation between them evolved very recently. This conclusion is complicated by the possibility that mitochondrial gene flow between species has erased more distant origins, but surveys indicate that all mtDNA haplotypes in the Strait of Georgia region are very young (Taylor et al. 1996). It is tempting to suppose that the larger degree of reproductive isolation between the coexisting species is at least partly a consequence of their degrees of habitat differentiation: speciation in Paxton Lake has led to two forms (limnetics and benthics) that exploit very different ecological environments, whereas the two old Pacific lineages (especially the marine forms) have no known ecological differences. With the possible exception of the white stickleback from Nova Scotia (Blouw and Hagen 1990), other apparently rapid cases of speciation with the *G. aculeatus* complex are also associated with habitat differences, such as marine and stream-resident species pairs (McPhail 1994). Possible mechanisms to explain the effects of habitat differentiation on speciation are discussed in the next three sections.

Natural Selection against Hybrids Has an Ecological Basis

The ultimate test of speciation is a demonstration that populations are able to coexist indefinitely in sympatry without collapsing to a single hybrid "swarm." Maintenance of discrete species is easy to understand if species never hybridize, but coexistence becomes precarious when hybrids are produced regularly. Limnetics and benthics probably hybridize in the wild: 1%–2% of adults collected in the field appear to be F_1 hybrids, as judged from morphological criteria, and this proportion changed little over a decade of sampling (McPhail 1984, 1992). However, no genetic markers for pure species and hybrids have yet been discovered, and so actual levels of gene flow are unknown. Any selection pressure that aids in forestalling collapse by removing hybrids is thus important to the speciation process. We conjectured that hybrids might be selected against in the wild simply because their intermediate morphology would render them less effective at obtaining food from the two main environments within lakes, littoral zone and open water (intermediate habitats are unknown). The conjecture was based on evidence that character displacement had occurred, implying that intermediate phenotypes in general are selected against in two-species lakes. It was tested by measuring growth rates of hybrids transplanted to the field and comparing these with hybrids raised in the laboratory, where trophic morphology should make little difference to fitness.

Offspring from crosses between limnetics and benthics grow in the laboratory at rates intermediate between those of the pure species (Hatfield 1995; J. D. McPhail, unpublished data), which suggests no intrinsic incompatibility between parental genomes. Viability, fertility, and male parental care are also high in F_1 hybrids, and levels of fluctuating asymmetry are the same as those in the parent species (Hatfield 1995). Fitness is somewhat diminished in both backcrosses, but not severely so, and no reduction was evident in the large sample of F_2 hybrids (Hatfield 1995). Therefore, evidence to date suggests no strong hybrid disadvantage in the laboratory.

In contrast, hybrids show a significant growth disadvantage when transplanted to the natural habitats in Paxton Lake (fig. 2). In the littoral zone their growth is poorer than that of benthics (although superior to limnetics'); in open water they do worse than limnetics. Averaged over habitats their growth is equal to or slightly below the average growth of limnetics and benthics. Thus, if hybrids and pure species choose to forage in the habitat where their expected growth is highest, wild hybrids should be substantially inferior. The pattern in figure 2 is based on a small sample of "F₁₀ hybrids" (fish collected from a population in a small lake established anew from F₁ hybrids 10 yr previously), but the effect was even stronger in a larger experiment involving F₁ hybrids (Hatfield 1995). Studies of individuals foraging in habitats transplanted to large aquaria showed that differences in growth rate among limnetics, benthics, and (F₁₀) hybrids stem from differences in foraging success (Schluter 1993, 1995a; see also Resources and Divergent Natural Selection). These differences in foraging success are associated in turn with the morphological differences between hybrids and parental species.

If our interpretation of growth patterns in hybrids in lab and field is correct, then divergent selection for efficient foraging in either the littoral zone or open water has led to their reduced fitness. This effect may be underestimated because our experiments have not yet included direct competition between hybrids and parental species for resources, which would be expected to further diminish the fitness of intermediates (see Divergent Character Displacement), nor do they incorporate differential risks of predation. It is therefore likely that resource-based selection pressures presently contribute to the maintenance of separate limnetic and benthic species in the face of some gene flow between them, and they thereby have contributed to the speciation process.

*Premating Isolation Partly Depends on Traits under
Divergent Natural Selection*

Mechanisms underlying the evolution of strong (though apparently still imperfect) premating isolation in the sticklebacks are obscure. However, two experiments suggest that mate choice leading to assortative mating is partly based on morphological traits that diverged in association with habitat differentiation, especially body size. Borland (1986) showed that marine (anadromous) and stream-resident sticklebacks breeding sympatrically in the lower section of the Salmon River, British Columbia, mated assortatively. This was in part because stream males preferred females equal to or smaller in size than themselves, which led to an avoidance of the larger marine females. Males living farther upstream, where marine sticklebacks are absent and mean size of freshwater females is greater, preferred to attract large females. In the other experiment, Nagel (1994; Schluter and Nagel 1995) showed that the probability of hybridization between limnetics and benthics from Paxton Lake was size dependent. The only heterospecific matings that took place in pairwise encounters between males and females of both species occurred between large females of the smaller species (limnetics) and small males of the larger species (benthics) and between large limnetic males and small benthic females.

A simple explanation for morphology-based assortative mating is that the mat-

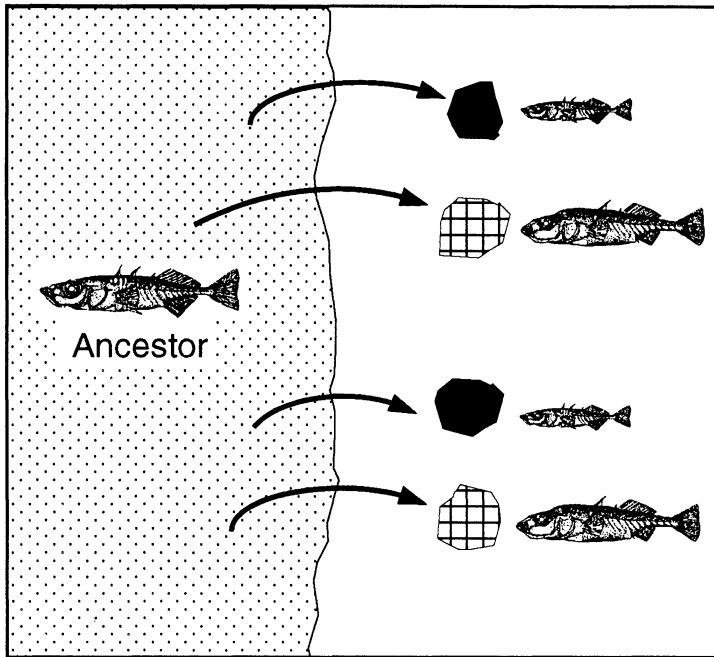


FIG. 6.—Example scenario for parallel speciation. Outlined areas are geographical ranges. Shading indicates environment type (e.g., habitat). Arrows indicate the establishment of new populations from a panmictic ancestral species. Colonization of two different types of environment leads to repeated divergence in morphology and in morphology-based mate preferences. (From Schluter and Nagel 1995.)

ing preferences diverged incidentally as a by-product of morphological differentiation (e.g., because of a genetic correlation between morphology and mate preference). More complex scenarios involving reinforcement cannot be ruled out. Size-based assortative mating is not uncommon between ecologically divergent species that differ in size. For example, it is also known from sockeye salmon (Foote and Larkin 1988), amphipods (Culver et al. 1994), and Galápagos finches (Ratcliffe and Grant 1983).

Parallel Evolution of Premating Isolation Indicates Natural Selection

Parallel evolution of independent, closely related lineages experiencing similar environmental conditions is perhaps the strongest nonexperimental evidence that evolution has occurred by natural selection (Clarke 1975). This principle is the basis of the modern comparative method in evolutionary biology (Harvey and Pagel 1991). By a similar logic, the repeated evolution of a specific mechanism of reproductive isolation in different related lineages under similar ecological circumstances (“parallel speciation”) is strong evidence that natural selection was the ultimate cause of speciation (Schluter and Nagel 1995). For example, an ancestral species may independently give rise to multiple new populations at the periphery of its range in two different types of environment (fig. 6). Parallel

speciation by natural selection occurs when reproductive isolation evolves between the descendant forms in different environments, but not between the separate populations living in the same type of environment.

The following results are suggestive of parallel speciation in sticklebacks because they fulfill some, but not all, of the necessary criteria (Nagel 1994; Schluter and Nagel 1995). The first line of evidence is indirect: marine sticklebacks have colonized fresh water independently multiple times (McPhail 1993; Bell and Foster 1994; fig. 5), and this has resulted in frequent parallel evolution of body size. Since body size is apparently a cue in mate choice (see *Premating Isolation*, above), it follows that mate preferences for small or large size have also evolved repeatedly in parallel. The second line of evidence is more direct and involved assessing degree of premating isolation between limnetic and benthic sticklebacks from different freshwater drainages. Nagel (1994; L. M. Nagel and D. Schluter, unpublished manuscript) showed that assortative mating between limnetics from different lakes (Paxton and Priest Lakes, Texada Island, British Columbia) was weak or absent. No assortative mating was detected between benthics from these same two lakes or between them and benthics from Enos Lake, Vancouver Island, British Columbia. In other words, fish of similar body size and shape and exploiting similar ecological environments have similar mate preferences. However, the admissibility of this evidence requires that reproductive isolation in separate species pairs evolved independently—widely believed, on the basis of geological evidence (Schluter and McPhail 1992; McPhail 1993), and supported by a molecular phylogeny, but needing further confirmation (Taylor et al. 1996). If independence of separate benthic and limnetic species pairs is borne out, then this would represent the first documented case of parallel speciation in nature (by mechanisms other than polyploidy) and provide strong evidence that natural selection directly or indirectly favored the evolution of reproductive isolation.

DISCUSSION

Surprisingly little empirical information from wild populations has accumulated on the roles of resource-based divergent selection and resource competition in adaptive radiation since an ecological theory of adaptive radiation was first developed decades ago. The present study attempted to address these issues using the ecologically diverse three-spined sticklebacks of coastal British Columbia.

A strong correlation among morphology, habitat use, feeding efficiency, and growth rate across populations is consistent with the idea that divergence in body form was driven by selection for efficient resource exploitation in alternative habitats. The trade-off between habitats in feeding efficiency and growth rate was steep. Few detailed data yet exist on the form of natural selection on morphology within habitats, except that small body size is probably favored in open water, judging from the relationship between feeding efficiency and size among individuals in this habitat (Schluter 1993).

Ecological character displacement was indicated by the large differences between sympatric species in morphology and ecology and the intermediate features of solitary species inhabiting lakes similar in size to those in which species pairs

are found. An experiment showed how natural selection on a solitary species favored a more benthic lifestyle after a planktivore was added. These results strongly support the hypothesis that divergence between closely related forms is partly driven by competitive interactions between them, as Lack (1947) and many of the other early naturalists maintained. The traits apparently under selection in the character displacement experiment are heritable in the wild (Hagen 1973; Baumgartner 1986; Schluter 1996), and one therefore presumes that such selection in nature would yield an evolutionary shift in subsequent generations. However, changes between generations have not yet been documented.

An additional question is whether the absence of competition from other taxa for resources (ecological opportunity) likewise affects rate and pattern of diversification. We have not yet investigated the role of other taxa but note that the most dramatic recent examples of rapid diversification in fish, including sticklebacks (see below), occurred in lakes that formed since the Pleistocene and that have been colonized by few other taxa (Schluter and McPhail 1993). A more comprehensive comparison with diversification rates in older, more species-rich lakes of unglaciated regions over the same time period is needed to test the hypothesis of ecological opportunity. Ultimately it would be desirable to directly measure the changes in natural selection on sticklebacks wrought by the presence/absence of other fish taxa.

Evidence for ecological speciation in sticklebacks is still incomplete, and this process is perhaps the least certain of the three components of the ecological theory. Nevertheless, several results hint of its importance: speciation was rapid and accompanied by divergence into different ecological niches; selection against hybrids is stronger in the wild than in the laboratory, which suggests that the ecological context is necessary to reveal hybrid performance; premating isolation depends in part on traits that diverged in association with exploitation of different resources; and reproductive isolation may have evolved in parallel in different populations experiencing similar environmental conditions.

In combination, these findings are highly consistent with a decades-old view of how adaptive radiation works, at least in its early stages when species diversity is low, and where diversification has been rapid. For sticklebacks, the traditional view is probably correct that competition played a major role in the evolution of ecological diversity. Preliminary indications are that ecological selection pressures indeed drove morphological diversification and speciation. Nevertheless, many details are still lacking and further tests are required. The value of these findings additionally depends on the extent to which they inform us about causes of adaptive radiation in general. How applicable are the findings to more species-rich radiations? I do not know the answer to this question, but consideration of two other radiations lends some confidence that the results here might apply to a wide variety of cases.

First, the radiation of sticklebacks is not unique but is duplicated to an almost uncanny degree by other fish taxa inhabiting post-Pleistocene lakes, especially salmonids (Schluter and McPhail 1993; Robinson and Wilson 1994). Lake-dwelling, sympatric pairs of species that show only slight amounts of genetic divergence are known in smelts (*Osmerus mordax* complex; Taylor and Bentzen

1991), Arctic char (*Salvelinus alpinus* complex; Hindar et al. 1986), brown trout (*Salmo trutta* complex; Ferguson and Taggart 1991), European whitefish (*Coregonus lavaretus* complex; Bernatchez and Dodson 1994), and lake whitefish (*Coregonus clupeaformis* complex; Bernatchez and Dodson 1991; Bernatchez et al. 1996). In virtually all such cases where ecological data are available, one of the two species of a given pair is pelagic and planktivorous, whereas the other species consumes littoral and benthic prey. Species pairs in different taxa are distinguished by similar suites of morphological features; for example, the planktivore is usually smaller and has a higher gill raker density than the more benthic species. In several cases (e.g., the smelts and lake whitefish; Taylor and Bentzen 1991; Bernatchez et al. 1996), the genetic data suggest that similar species pairs have arisen multiple times independently within each of these lineages. Morphological studies of other species pairs indicate that the phenomenon is widespread and that many other examples exist. The resemblance of these other cases to limnetic and benthic sticklebacks hints strongly that similar processes to those described in the sticklebacks may underlie patterns of diversification in these other fish groups. Similar environmental circumstances evidently lead to replicate trends in adaptive radiation, at least in north-temperate fishes.

Second, the results of our preliminary studies in the sticklebacks are strikingly reminiscent of processes identified in the Galápagos ground finches, the most comprehensive field study yet of an adaptive radiation (Grant 1986). In that study, divergent selection between populations and species of ground finches (*Geospiza*) is driven by availability of seeds of different size and hardness and by ecological character displacement. The role of resources is indicated by direct measurements of fluctuating selection on single populations faced with a changing food base (Gibbs and Grant 1987; Grant and Grant 1989) and by the close match between observed mean beak sizes on islands and those predicted from island-specific seed size/hardness distributions (Schluter and Grant 1984). Character displacement is indicated by comparisons of species in sympatry and allopatry and by discrepancies between observed and predicted mean beak sizes when food supply alone (i.e., without competition) is used to generate predictions (Schluter et al. 1985). The role of these ecological forces in speciation is less well understood than their role in morphological differentiation, but several aspects of the biology of reproductive isolation in the finches match those of the present study. For example, hybrid fitness strongly depends on resource distribution (relative availability of small and large seeds; Grant and Grant 1992), and mate choice depends on trophic morphology (absolute and relative beak and body size; Ratcliffe and Grant 1983).

Interest in the phenomenon of adaptive radiation is increasing, and eventually it will be possible to make a more comprehensive assessment of the generality of these findings. At present most new information on adaptive radiation is coming from phylogenetic studies: accurate trees of phylogenetic relationship between descendant species that are based on traits other than the phenotypic dimensions ostensibly under natural selection (i.e., molecular data; Givnish and Sytsma 1996); phylogeny-based comparative tests of the association among interspecific variation in morphology (and physiology and behavior), performance, and niche use (e.g., Losos 1990; Richman and Price 1992; Miles 1994); reconstruc-

tions of ancestral trait values, which generate a picture of the sequence of steps in a given adaptive radiation (e.g., Losos 1992); and comparative study of rates of speciation between sister taxa exploiting different types of resources (e.g., Mitter et al. 1988). All of these directions are likely to contribute to a better knowledge of the ecological forces that drive diversification. For example, comparative tests of hypotheses such as parallel speciation are impossible without accurate phylogenies.

Yet, efforts to understand the ecological causes of diversity lag far behind phylogenetic and historical descriptions of this diversity. Basic ecological information (e.g., niche relationships, competition, predation, hybrid fitness in the wild) is lacking for even some of the most spectacular adaptive radiations, such as the cichlid fishes of East Africa and the drosophilid flies of Hawaii. Ecological studies are the key to understanding mechanisms of divergent selection and the evolution of reproductive isolation.

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