

ADAPTIVE RADIATION IN STICKLEBACKS: TRADE-OFFS IN FEEDING PERFORMANCE AND GROWTH¹

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Abstract. Divergent natural selection for efficient exploitation of alternative resources is thought to be a primary cause of adaptive radiation. I transplanted two recently diverged stickleback species (*Gasterosteus* sp.) and their Hybrids between habitats to test three predictions of this hypothesis: (1) the form of natural selection on feeding traits should differ between resource environments; (2) fitness trade-offs should occur between morphs specialized for different resources; (3) feeding efficiency should be the basis of fitness differences between morphs. Growth rate was used as a surrogate component of fitness. All three predictions were upheld. The larger of the two species (the Benthic), which has a larger mouth, deeper body, and fewer, shorter gill rakers than the second species (the Limnetic), had a twofold growth advantage in the littoral zone of the lake. This pattern was reversed in the open-water habitat, where the Limnetic species grew at double the rate of the Benthic. Hybrids, which are morphologically intermediate, tended to be intermediate in growth in both habitats. Growth rates were closely predicted by earlier laboratory measurements of feeding efficiency of the three forms in the same habitats, thus linking growth (and probably fitness) with feeding performance and morphology. I compare the strengths of the present approach with other methods that have been used to test the role of resources in adaptive radiation. I also argue that steep trade-offs in fitness along the littoral–open-water habitat gradient have two further consequences. First, they may cause Hybrids to have low fitness, allowing Benthics and Limnetics to coexist in the absence of perfect premating isolation between them. Second, they may promote ecological character displacement. Steep trade-offs may thus help explain why divergence along the littoral–open-water gradient is so common in fish that have colonized low-diversity lakes.

Key words: adaptive radiation; British Columbia; growth trade-offs; habitat selection; performance and fitness; sticklebacks.

INTRODUCTION

Divergent natural selection between populations exploiting different resources is hypothesized to be a primary cause of adaptive radiation (Lack 1947, Amadon 1950, Mayr 1963, Bock 1970, Fryer and Iles 1972, Schluter and Grant 1984, Futuyma 1986, Grant 1986, Schluter 1993). Divergent selection is thought to be generated in turn by the advantages of alternative body forms for efficiently exploiting these resources. This hypothesis of adaptive radiation makes at least three empirical predictions.

First, the form of selection on trophic traits should differ in different resource environments. Second, feeding efficiency should be the basis of fitness differences between morphs. These two predictions, if borne out, would fulfill Arnold's (1983) chain of evolutionary causes (morphology → [feeding] performance → fitness) over several resource environments. Few studies have accomplished this feat. Comparisons of selection on single populations in fluctuating food environments (Boag and Grant 1981, Gibbs and Grant 1987, Grant

and Grant 1989, 1993) meet the two predictions most closely.

Third, trade-offs should occur between the fitnesses of morphs specialized for different resource environments. That is, morphological adaptations to exploiting one resource should decrease fitness on other resources. The reasoning behind this principle is that if a single body form is best suited to exploiting all resources, then little diversification is expected to ensue.

Here I test the above predictions in two sympatric, morphologically distinct species of sticklebacks (*Gasterosteus* spp.) and their Hybrids. The fish are part of a complex of new species that inhabit small young lakes (<13 000 yr) along the Canadian west coast (Schluter and McPhail 1992, McPhail 1993). In every lake where a pair of species is found, one of the species (the Limnetic) feeds on plankton in the open-water zone, whereas the other (the Benthic) chiefly exploits prey from the sediments or attached to vegetation in the littoral zone. Their morphological differences are largely genetically based, and correlate with their differences in habitat and diet. Populations occurring alone in lakes are intermediate between Limnetics and Benthics in morphology and habitat, suggesting that divergence between sympatric species was driven in part by inter-

¹ Manuscript received 8 November 1993; revised 15 April 1994; accepted 26 April 1994; final version, received 17 May 1994.

specific resource competition (i.e., character displacement). The complex appears to represent an adaptive radiation in its earliest stages.

The question of whether the two habitats (open-water and littoral zones) present distinct selective environments is especially intriguing because such selection may be involved in the speciation process itself (Schluter and McPhail 1992). Interspecific Hybrids are viable and fertile in the laboratory (McPhail 1984, 1992; T. Hatfield, *unpublished data*) and are occasionally produced in the wild (McPhail 1984, 1992). It is not unlikely that a species pair would collapse to a single hybrid form without distinctive selection pressures between habitats. Long-term persistence of a species pair is then most likely when trade-offs are steep, such that fitnesses of alternative extreme morphs cross between environments (Rausher 1984a, b). The presence and form of trade-offs in sticklebacks were thus of interest.

In an earlier laboratory study I showed that trophic morphologies of two sympatric species and their hybrids predict feeding efficiencies in the two habitats (Schluter 1993). The present paper compares growth rates, a surrogate component of fitness, of the same forms in a reciprocal field transplant. Though growth rate is not strictly a fitness component it has many positive fitness consequences in fish. These include higher overwinter survival (Shuter and Post 1990, Conover 1992), higher fecundity (Bagenal 1978; Fig. 1) and earlier breeding (Schultz et al. 1991, and references therein). Most of these advantages are mediated through the effects of growth rate on subsequent body size.

METHODS

Species and study site

The experiment was carried out on the two species of sticklebacks coexisting in Paxton Lake, Texada Island, British Columbia. The species are not yet formally described and are referred to as Benthic and Limnetic, on the basis of their preferred feeding habitats. McPhail (1992) and Schluter (1993) summarize evidence that the two forms are true biological species rather than alternative morphs of a single-species polymorphism. F₁ Hybrids between them are viable and fertile when raised in the laboratory (McPhail 1984,

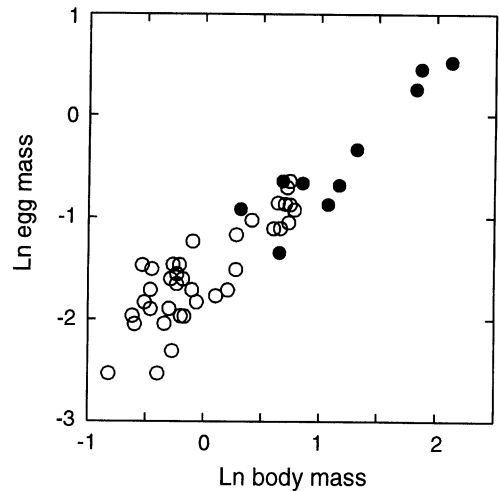


FIG. 1. Fecundity (total mass of eggs) of females in relation to body mass. Data are from Paxton Lake Benthics (●) and Limnetics (○). Mass of eggs and females was measured in grams immediately after eggs were manually stripped from gravid females.

1992; T. Hatfield, *unpublished data*). However, as a precaution against any temporary F₁ Hybrid vigor or inferiority, I used individuals from Second Lake, Texada Island, where a population was established from F₁ Hybrids in 1980 (J. D. McPhail, *personal communication*). The population has remained morphologically intermediate between Limnetics and Benthics in every known respect over 11 subsequent generations.

The two species differ in size (Table 1) and shape: Limnetics are more slender and narrow-mouthed than Benthics, and possess longer, more numerous gill rakers (Larson 1976, McPhail 1992, Schluter and McPhail 1992, Schluter 1993). Rakers are protuberances along the gill arches that function to sieve small particles of prey (e.g., plankton) or to redirect them by altering water currents in the buccal cavity (Sanderson et al. 1991). Number and length of gill rakers is predictably associated with degree of planktivory in fish in general (Hyatt 1979, Schluter and McPhail 1993).

Transplant experiment

I carried out the experiments in spring (April and May) of 1991 and 1992. A total of 36 enclosures was

TABLE 1. Mean body length and mass of the three forms (± 1 SD). The first column of numbers is from a random sample of 40 individuals of each species from May 1989. Measurements from the present study were taken at the start of each experiment. Sample sizes were 12 of each form in 1991 and 18 of each form in 1992.

	Standard length (mm)						Body mass (g)			
	Paxton Lake		Present study				Present study			
			1991		1992		1991		1992	
Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Benthic	53.6	6.6	43.7	2.7	46.1	4.0	1.06	0.28	1.42	0.47
Hybrid	42.3	2.5	0.92	0.20
Limnetic	43.8	6.4	39.9	1.9	40.3	2.9	0.74	0.12	0.78	0.21

TABLE 2. Diet of fish at the end of the 1992 experiment. Prey proportions are based on the combined sample of items from all stomachs; as individual items are not independent, standard errors cannot be computed. Remaining quantities are means of $N = 9$ individuals per sample. Standard errors are in parentheses.

Prey type	Diet proportions			
	Littoral zone		Open water	
	Limnetic	Benthic	Limnetic	Benthic
Insect larvae	0.18	0.24	0.08	0.11
Amphipods	0.06	0.08	0.01	0.02
Ostracods	0.30	0.25	0.02	0.03
Copepods	0.30	0.29	0.80	0.64
Cladocerans	0.17	0.15	0.09	0.21
Mean number of items	24.1 (5.5)	29.0 (6.3)	61.7 (23.0)	54.8 (15.5)
Mean prey length (mm)	1.09 (0.18)	1.78 (0.34)	1.13 (0.18)	1.18 (0.14)

used each year, 18 in each of the two habitats, littoral zone and open water. The littoral zone is the primary area exploited by Benthics in spring (Larson 1976; D. Schluter 1993, *unpublished data*). The open water represents the plankton environment, which is exploited intensively by Limnetics. Limnetics also use the littoral zone, particularly in spring when males establish breeding territories in the shallows (Larson 1976, Schluter 1993).

Enclosures were constructed of durable knotless nylon mesh (0.6 cm pore size). Littoral enclosures were 1×1 m square pens 1.5 m high with open bottoms, set in water of ≈ 1 m depth. They were placed haphazardly along the margins of the south basin of the lake. Wild fish were removed from enclosures using a minnow trap or dip net prior to the start of the experiment. Open-water enclosures were cylindrical columns of mesh supported by metal rings, 1 m in diameter, 6 m deep, and closed at the bottom. This depth was sufficient to penetrate the early summer thermocline, and allowed migration of plankton within the bags and across the mesh boundary. The columns were suspended in rows from styrofoam floats near the deepest part (10 m) of the south basin of the lake.

The fish used in the experiments were obtained from Paxton and Second Lakes ≈ 1 wk prior to the study, and were maintained and fed in the laboratory. When collecting fish, I selected relatively small individuals to ensure that substantial growth was still possible. For this reason, the experimental fish were smaller in size than a random sample (Table 1). I also attempted to ensure overlap in size between the species, which resulted in a lesser size difference between them than in a random sample (Table 1). The effects of initial size on growth rate were tested at the end of the experiment.

Fish were assigned randomly to habitat treatments. A single individual was released into each enclosure; each fish is therefore an independent replicate. Individuals were weighed to within 0.01 g using a portable balance (Ohaus CT 200, Ohaus Corporation, Florham Park, New Jersey, USA) immediately prior to being released. The experiment was terminated 21 d later.

Recaptured fish were weighed immediately, and then anaesthetized and preserved in 35% isopropyl alcohol.

The experiment was carried out twice, on 14 May 1991, and on 16 April 1992. Dates represented early to middle of the breeding season of Benthics, and early in the breeding season of Limnetics. None of the fish used in the experiments was in breeding condition at the start of the study, although several were by its termination; deleting these had no detectable effect on the findings. In 1991, the experiment was carried out on six individuals per habitat and species of Benthics, Limnetics, and Hybrids. Standard errors of mean growth rates were large, and to obtain better estimates of growth rates of the parent species I used only Limnetics and Benthics in 1992 (nine fish per habitat and species). No mortality occurred in 1991. In 1992, three Benthics and one Limnetic died or disappeared, all from the littoral zone. Since sample size is least for Hybrids, less confidence can be attached to estimates of their growth.

Two potential artifacts of the experiment need to be addressed. First, calanoid copepods, one of the main open-water prey items in the diet of wild Limnetics, abandoned the open water enclosures. Supplementing the bags with calanoids could not forestall this effect. Second, the pens in open water acted as a substrate for benthic algae and invertebrates, which gradually colonized during the experiment. Both these problems were minimized by carrying out the study in spring, when calanoids do not yet constitute a major portion of the Limnetic diet (Schluter 1993), and when settlement rate of benthic organisms was found to be lowest. The second problem was also minimized by limiting the study's duration to 3 wk.

RESULTS

Experimental diets

Within each habitat, diet proportions of both species were similar (Table 2). Planktonic prey (mainly cyclopoid copepods) predominated in open water. Littoral zone diets were dominated by insect larvae (mainly

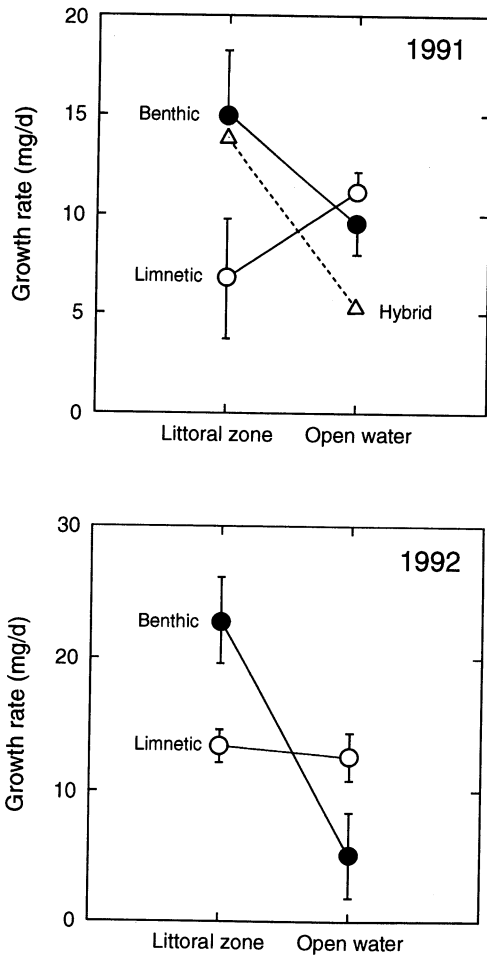


FIG. 2. Mean growth rates of species in the two habitats in both years. Solid lines connect means for the Benthic (●) and Limnetic (○) species. Dashed line connects means for interspecific hybrids. Vertical bars are ± 1 SE; only one is drawn if points are in close proximity. SE's for Hybrids (Δ) were omitted for clarity, but were similar in magnitude to those for the pure species. Hybrids were tested in 1991 only. $N = 6$ for each mean in 1991. $N = 9$ for each mean in open water in 1992; in the littoral zone $N = 8$ Limnetics and $N = 6$ Benthics.

midge larvae), ostracods, and copepods (mainly benthic cyclopoids).

Habitat and species differences

Growth of the two species exhibited a "crossed" pattern over habitats (Fig. 2), and corresponded with their morphological differences. Benthics grew consistently better in the littoral zone than in open water. Growth of Limnetics was roughly equal between habitats in 1992, and may have been higher in the open water habitat in 1991 (the change is not significant). In both years, Benthics were substantially superior to Limnetics in the littoral zone, but were inferior in open water (Fig. 2). Hybrids tended to be intermediate,

though they may have been inferior to both species in open water.

Overall effects of year, habitat, and species were compared using three-way ANOVA (Hybrids excluded; Table 3). The most dramatic effects were a higher overall mean growth rate in the littoral zone than in open water (as indicated by a habitat main effect), and the crossed pattern of fitnesses over habitats (as reflected in the strong habitat \times species interaction; Fig. 2). This interaction was significant in each year analyzed separately. Superior overall growth in the littoral zone, averaged across species, was evident only in 1992. No other interactions were tested, to preserve degrees of freedom and in the absence of a priori expectations. A moderate but nonsignificant difference between years was observed in mean growth rates (Table 3). No significant differences were detected among species, implying that each did roughly equally well when growth was averaged across habitats.

Separate two-way analyses were carried out to explore variation between years in factor effects (Hybrids excluded). Growth was significantly different between species in both habitats analyzed separately ($F_{1,22} = 11.31$, $P = 0.003$ and $F_{1,26} = 4.58$, $P = 0.042$ for littoral zone and open water, respectively). In neither analysis was there indication that the magnitude of the difference between the two species varied between years (year \times species interactions for the two habitats separately: $F_{1,22} = 0.002$, $P = 0.97$, and $F_{1,26} = 1.42$, $P = 0.25$). Separate analyses for each species revealed that growth differences between habitats were significant in Benthics ($F_{1,23} = 13.73$, $P = 0.001$) but not in Limnetics ($F_{1,25} = 1.50$, $P = 0.23$). There was a hint of variation between years in the magnitude of the habitat difference (Benthics: $F_{1,23} = 3.87$, $P = 0.061$; Limnetics: $F_{1,25} = 2.61$, $P = 0.119$).

Fitness trade-offs

Reversals between species in the profitability rankings of habitats imply a fitness trade-off: adaptations to improve growth in one habitat have evolved at the expense of reduced success in the second. This trade-off is best illustrated by a "fitness set" combining measurements from both years (Fig. 3). The dashed line connecting means for the two parent species highlights

TABLE 3. ANOVA of growth rates. Effect refers to the square root of the corresponding variance component, and measures variation in growth (mg/d) between factor levels. This analysis excludes the 1991 hybrids, but results are very similar if they are included.

Source	Effect	df	MS	F	P
Year	1.22	1	120	2.3	0.133
Habitat	2.43	1	357	7.1	0.010
Species	0.60	1	60	1.2	0.286
Habitat \times species	3.50	1	718	13.9	0.001
Error	...	51	52

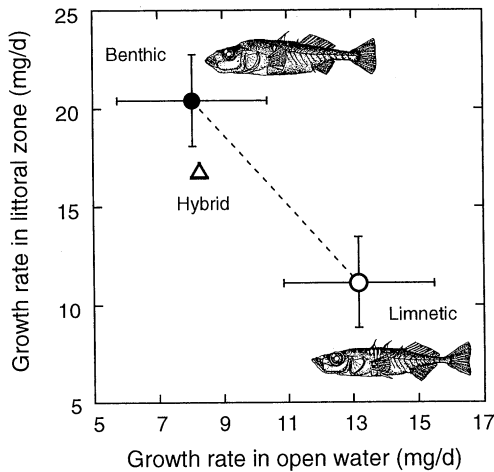


FIG. 3. Trade-off in growth rate between habitats. Symbols indicate species means \pm 1 SE. The means are corrected for differences between years, by adding 3.0 units to all the 1991 values, which is the difference between 1992 and 1991 in the average growth rate of Limnetics and Benthics. Hybrid SE's were omitted for clarity.

the negative correlation between growth rates of the extreme body forms in the two habitats.

Overall, the relative benefits of alternative specializations were twofold and symmetric (Fig. 3): Benthics grew at roughly twice the rate of Limnetics in the littoral zone, whereas Limnetics outperformed Benthics in the open water habitat by an approximately twofold margin.

The dashed line in Fig. 3 is a useful reference for assessing the fitness of intermediate phenotypes (e.g., Hybrids). Were the fitness of intermediates in the littoral zone as high as Benthics, and in open water as high as Limnetics, then mean growth of Hybrids would lie toward the upper right corner in Fig. 3 at the hypothetical point $(X, Y) = (13, 20)$. In contrast, intermediate phenotypes would suffer a competitive disadvantage if mean growth was displaced from this hypothetical point toward the origin. This is because the Hybrid would be poorer than the Benthic in the littoral zone and poorer than the Limnetic in open water. The dashed line demarcates a fitness boundary below which intermediate phenotypes, averaged across habitats, have a growth rate less than the average of the parent species.

Mean growth rate of Hybrids fell below the demarcation line (Fig. 3), though this estimate is highly tentative. It is based on a small sample size, and is not significantly different from means of either parent species. However, the result is the second independent indication that Hybrids suffer substantially lower performance than the parent species; an earlier study revealed that feeding success of Hybrids in the same two habitats was lower than the average feeding success of Benthics and Limnetics (Schluter 1993).

Feeding performance and growth rate

Growth differences among forms in the two habitats were as predicted from their morphological differences. It remains to be established whether differences in feeding performance are responsible for this association. To test this I compared field growth rates in the present experiment to laboratory estimates of net energy intake in the same two habitats (Fig. 4; data from Schluter 1993). Net energy intake was calculated in 1990 from capture and handling times of natural prey in littoral and open-water habitats transplanted to large aquaria. The benthic aquarium presented an equivalent surface area of lake sediment taken from the littoral zone at various depths above the thermocline. The open-water aquarium presented the contents of dusk plankton tows at ambient prey mixtures and densities (Schluter 1993). The estimates subtract energy requirements for maintenance. A larger range of body sizes of fish was represented than in the present experiment, and mean sizes were slightly larger (by 1–2 mm in length).

Feeding performance calculated in this way strongly predicted growth rate across habitats and species (Fig. 4; $r = 0.87$, $P = 0.026$; this P value is tentative because points may not be strictly independent). For example, the high growth rate of Benthics in the littoral zone matched its high feeding rate there; conversely, both its growth rate and estimated net energy intake were low in open water. Growth of Limnetics was relatively

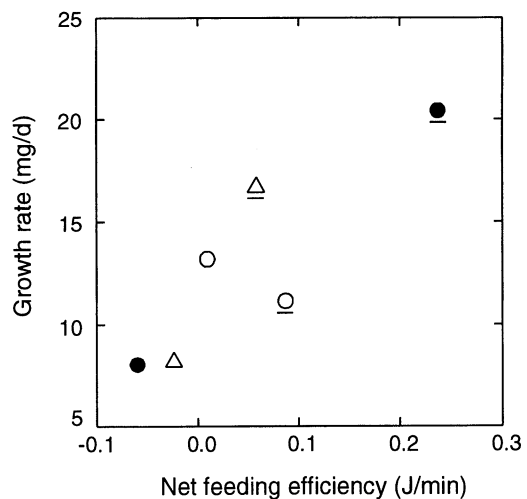


FIG. 4. Relationship between growth rate measured in the present experiment (Y axis) and laboratory measurements of feeding efficiency of the same species and in the same two habitats (data from Schluter 1993). Feeding efficiency is median energy intake rate while foraging (estimated intake rate minus energy required for body maintenance). It was estimated by monitoring individual fish foraging in large aquaria containing transplanted natural habitat. Species symbols are as in Fig. 2. Two points are given for each species, one for the littoral zone (underlined) and one for the open-water zone. Mean growth rates are corrected for differences between years as described in Fig. 3.

similar in the two habitats, as was feeding performance. The Hybrid pattern was like that of the Benthic, but differences between habitats were less extreme. The association between growth and feeding performance held not only across habitats but among species: Limnetics and Hybrids were intermediate between the Benthic extremes in both measures.

These results support the conclusion that differences in growth among both habitats and species can be attributed to differences in foraging success. Foraging success can be attributed in turn to differences in body form (Schluter 1993). The present data thus corroborate the hypothesized chain of causes: morphology → feeding performance → fitness (via growth rate).

Body size

The stickleback species differ in body size (Table 1) as well as shape (Schluter 1993), and it would be useful to know the relative importance of each to growth. The current data are somewhat inconclusive because the full range of body sizes was not investigated (Table 1), and because the correlation between initial size (ln-transformed body mass) and subsequent growth was not strong (excepting Benthics in open water, $|r| = 0.64$; other $|r| = 0.06$ – 0.10). To explore the role of size I carried out an additional analysis similar to that of Table 3, using year-corrected growth rates in place of the year factor (see Fig. 3), and adding the continuous variable ln(initial body mass). As before, Hybrids were excluded.

Two results were clearest. First, the effect of size was not significant in any comparison except the three-way interaction between size, habitat, and species ($F_{1,50} = 4.79$, $P = 0.033$; interaction terms involving size were included one at a time in a series of separate ANOVAs). This resulted mainly from the observation that regressions of growth on size had low positive slopes when each species was in its own habitat (i.e., Benthic in the littoral zone and Limnetic in open water; pooled slope = 1.98 ± 5.02 SE) but had negative slopes when each species was in the other's habitat (pooled slope = -13.0 ± 4.54 ; difference between pooled slopes = 15.0 ± 6.77 , $t_{50} = 2.211$, $P = 0.040$). The upshot is that size's role within a given habitat depends on the species, and this is probably because species differ in body shape. In other words, size alone cannot account for differences between species in growth rates.

Second, adding size did not alter the main finding of the earlier ANOVA model (Table 3). Accounting for the three-way interaction involving size merely strengthened the trade-off in growth rates of species between habitats ($F_{1,50} = 18.1$, $P < 0.001$). However, the average difference in growth between habitats was no longer large ($F_{1,50} = 0.49$, $P = 0.49$).

DISCUSSION

Diversification in morphology, feeding performance, and fitness

Divergent natural selection for efficient exploitation of alternative resources is thought to underly adaptive radiation. Four kinds of tests of this hypothesis are possible. To put the present results into perspective, it is worth summarizing these four approaches and their strengths.

1. *Correlation between morphology and resource use.*—This step is the easiest and usually the first in an ecological study of adaptive radiation. It is therefore the most frequent test of divergent natural selection. Recent examples include Grant (1986), Huey and Bennett (1987), Richman and Price (1992), and Schluter and McPhail (1992). New, phylogeny-based methods (Felsenstein 1985, Harvey and Pagel 1991) are transforming the way that such correlations are measured (Huey and Bennett 1987, Richman and Price 1992). Nevertheless, such correlations constitute relatively weak evidence on their own. This is because a wide variety of ecological differences between species may be correlated with morphology, yet only a minority of these may have been responsible for their diversification.

2. *Correlation between morphology and resource use efficiency.*—Stronger evidence for divergent selection is given by a demonstration that morphologically different forms vary in their abilities to exploit resources, and that each species prefers the resource yielding highest intake rates. The advantage of such comparisons is that they directly test the mechanism of resource use efficiency that is central to the hypothesis of adaptive radiation. Recent examples comparing species or morphs in their performance on different resources include Lavin and McPhail (1986), Huey and Bennett (1987), Smith (1987), Ehlinger (1990), Losos (1990), Norton (1991), Sinervo and Losos (1991), Malmquist (1992), Benkman (1993), and Schluter (1993). Several of these studies have additionally demonstrated trade-offs in performance between resource environments (e.g., Benkman 1993). The most powerful studies incorporate experimental manipulation of individual traits to measure their direct effects on use efficiency (Drenner et al. 1987, Benkman and Lindholm 1991). The only drawback to this approach is that several aspects of performance may be correlated with morphology (e.g., prey capture rate, predator escape speed, quality of nest construction), and one must still infer which of these was most important to fitness.

3. *Estimation of adaptive landscapes.*—This method combines the measured relationship between morphology and performance with information on resource availability, to estimate a priori the dependence of fitness on body form. Optimal size and shape is that value corresponding to a peak in the estimated fitness surface.

This approach is very powerful because, of the four methods listed here, it alone makes quantitative predictions of species size and shape from the hypothesized mechanism of adaptive radiation. Examples are rare, perhaps because of the large amount of information needed (e.g., usually one needs good estimates of resource availability). Applications of this approach have shown that (1) morphologies of species often correspond to peaks in the fitness surface (Schluter and Grant 1984, Schluter et al. 1985, Benkman 1993; but see Armbruster 1990); (2) more than one optimal phenotype may exist in a given environment (Schluter and Grant 1984, Schluter et al. 1985); and (3) predicting morphology of any one species may require that competition from other species is taken into account (Case 1979, Schluter and Grant 1984, Schluter et al. 1985).

4. *Correlation between morphology and fitness.*—This method directly compares fitness (or, more usually, a fitness component) of a range of morphs across two or more resource environments. The clearest examples demonstrate that (1) the phenotype having highest fitness changes between resource environments; and (2) feeding performance on the changing availability of resources is the probable cause of differences between environments in fitness. Direct fitness comparisons thus provide among the strongest tests of the hypothesis that divergent natural selection underlies adaptive radiation. Examples are rare, and come almost entirely from studies of Darwin's finches (Boag and Grant 1981, Gibbs and Grant 1987, Grant and Grant 1989, 1993). Several other studies have compared fitness components of species or host races transplanted across habitats or environments (e.g., Rausher 1984a, Pashley 1988, Bierbaum and Bush 1990, Fry 1990, Jordan 1991, Via 1991, Trexler et al. 1992), but the morphological and performance mechanisms leading to differences in fitness are usually unknown.

The present study, in combination with earlier work, has used a combination of approaches 1, 2, and 4 (using growth rate as a surrogate component of fitness). Thus far the work has shown that (1) morphological differences between populations and species are strongly linked to differences in use of two main habitats (Schluter and McPhail 1992); (2) these morphological differences are associated with trade-offs in the efficiencies of food exploitation between habitats (Schluter 1993); (3) growth rates (and probably fitnesses) of the two species also trade-off between habitats, and are closely predicted by feeding performance; and (4) Hybrids tend to be intermediate in morphology, feeding performance, and growth, and may be at a selective disadvantage for this reason. These results strongly support the conclusion that selection for efficient use of alternative food resources is the cause of adaptive radiation in sticklebacks. They also support the principle that adaptation to alternative resources is governed by fitness trade-offs. Further work should gain a more accurate measure of the form of natural selec-

tion within each habitat, and a finer assessment of the fitnesses of intermediate phenotypes, using smaller increments of morphology.

Note that individuals were tested in isolated enclosures, with the result that immediate effects of species interactions on performance and growth could not be measured (longer term effects may have been incorporated through prior effects of the two species on the distribution of resources available in the lake). If species compete (Schluter and McPhail 1992) then the present study may have underestimated the magnitude of trade-offs between habitats. For example, aggression or rapid resource depletion by Benthics in the littoral zone may explain why Limnetics use mainly the open-water habitat in summer, even though their performance and fitness there (measured in isolation from Benthics) appears to be little greater than in the littoral zone (Schluter 1993; Fig. 2). Direct tests of competition between Limnetics and Benthics are in progress.

Adaptive radiation in sticklebacks

The present study leaves open at least three additional questions about this adaptive radiation. First, what role do divergent selection pressures play in speciation? This question has been chiefly raised in other systems with reference to sympatric speciation (Diehl and Bush 1989, Grant and Grant 1989, Wilson 1989), which may be unlikely in the sticklebacks (Schluter and McPhail 1992, McPhail 1993). Yet, even if species form allopatrically they may produce viable and fertile hybrids when they later become sympatric. Sharply contrasting selection pressures between their distinct ecological environments may then be the main cause of low hybrid fitness, and hence would be necessary for species persistence in the absence of perfect pre-mating isolation. This situation is most likely to pertain when species are very young (e.g., the sticklebacks), because older species will inevitably have accumulated intrinsic postmating barriers to gene flow (Coyne and Orr 1989). The sticklebacks present a tractable system in which to test these ideas because of the opportunities for experimental perturbation.

Second, if intermediate phenotypes are at a disadvantage, why are solitary populations of sticklebacks intermediate in morphology? There are two possible explanations. One is that solitary populations are indeed under disruptive selection, but they are maintained at an intermediate position by rare-phenotype advantage. For example, if a solitary population were to evolve for a time toward a more benthic morphology, depletion of benthic resources would cause planktivorous individuals to be favored, because they are more rare and their resources are less depleted. The population would then evolve back toward an intermediate phenotype. This mechanism is at the core of the Wilson-Turelli model of frequency-dependent natural selection (see Wilson 1989). The other possible explanation is that in a single-species lake intermediate

phenotypes are optimal. That is, a solitary species may gain by being a generalist, particularly as it could take advantage of peaks in resource abundance in both habitats, which occur at different times in the season (e.g., Schluter 1993). Intermediate phenotypes would have low fitness only when resources in the two main habitats are depleted by separate littoral and open-water specialists. Distinguishing these alternatives is a major goal of future research.

Finally, why has diversification taken place along the littoral–open-water habitat gradient rather than some other resource gradient (e.g., insectivore–piscivore)? This question is not limited to sticklebacks: the littoral–open-water gradient is the commonest mode of diversification in lake fishes (Schluter and McPhail 1992, Robinson and Wilson 1994). The answer may be related to the one above: coexistence of newly formed species may require sharp trade-offs in fitness between resources. However, steep trade-offs along the littoral–open-water gradient may bias the direction of diversification for another reason. Morphological divergence in sticklebacks and many other groups probably represents ecological character displacement (Schluter and McPhail 1992, 1993, Robinson and Wilson 1994). According to theory (Taper and Case 1985) character displacement is most likely when an increment of morphological divergence yields a large reduction in the intensity of interspecific competition, and a small reduction in the total availability of food to each competitor. The steep trade-off along the littoral–open-water gradient means that a single morphology cannot efficiently monopolize the full spectrum of resources. Hence this axis may be particularly favorable to character displacement.

Fish in postglacial lakes present some of the youngest examples of adaptive radiation on earth (Schluter and McPhail 1993). Because of their experimental tractability, the sticklebacks and similar groups present among the best opportunities to study its ecological basis.

ACKNOWLEDGMENTS

Thanks to T. Hatfield, G. Mittelbach, L. Rowe, and the two reviewers for their comments on the manuscript, and to T. Day, T. Hatfield, T. Law, L. Nagel, and J. Pritchard for help in the field. H. Diggon graciously provided access to Paxton Lake. This work was funded by NSERC (Canada).

LITERATURE CITED

- Amadon, D. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). *Bulletin of the American Museum of Natural History* **95**:151–262.
- Armbruster, W. S. 1990. Estimating and testing the shapes of adaptive surfaces: the morphology and pollination of *Delachampia* blossoms. *American Naturalist* **135**:14–31.
- Arnold, S. J. 1983. Morphology, performance and fitness. *American Zoologist* **23**:347–361.
- Bagenal, T. B. 1978. Aspects of fish fecundity. Pages 75–101 in S. D. Gerking, editor. *Ecology of freshwater fish production*. Wiley, New York, New York, USA.
- Benkman, C. W. 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. *Ecological Monographs* **63**:305–325.
- Benkman, C. W., and A. K. Lindholm. 1991. An experimental analysis of the advantages and evolution of an evolutionary novelty. *Nature* **349**:519–520.
- Bierbaum, T. J., and G. L. Bush. 1990. Genetic differentiation in the viability of sibling species of *Rhagoletis* fruit flies on host plants, and the influence of reduced hybrid viability on reproductive isolation. *Entomologia Experimentalis et Applicata* **55**:105–118.
- Boag, P. T., and P. R. Grant. 1981. Intense natural selection in a population of Darwin's ground finches (Geospizinae) in the Galápagos. *Science* **214**:82–85.
- Bock, W. J. 1970. Microevolutionary sequences as a fundamental concept in macroevolutionary models. *Evolution* **24**:704–722.
- Case, T. J. 1979. Character displacement and coevolution in some *Cnemidophorus* lizards. *Fortschritte der Zoologie* **25**:235–282.
- Conover, D. O. 1992. Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology* **41B**:161–178.
- Coyne, J. J., and A. Orr. 1989. Patterns of speciation in *Drosophila*. *Evolution* **43**:361–381.
- Diehl, S. R., and G. L. Bush. 1989. The role of habitat preference in adaptation and speciation. Pages 345–365 in D. Otte and J. A. Endler, editors. *Speciation and its consequences*. Sinauer, Sunderland, Massachusetts, USA.
- Drenner, R. W., G. L. Vinyard, K. D. Hambright, and M. Gophan. 1987. Particle ingestion by *Tilapia galilaea* is not affected by removal of gill rakers and microbranchiospines. *Transactions of the American Fisheries Society* **117**:272–276.
- Ehlinger, T. J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. *Ecology* **71**:886–896.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**:1–15.
- Fry, J. D. 1990. Trade-offs in fitness on different hosts: evidence from a selection experiment with a phytophagous mite. *American Naturalist* **136**:569–580.
- Fryer, G., and T. D. Iles. 1972. *The cichlid fishes of the great lakes of Africa*. T.F.H. Publications, Neptune City, New Jersey, USA.
- Futuyma, D. J. 1986. *Evolutionary biology*. Second edition. Sinauer, Sunderland, Massachusetts, USA.
- Gibbs, H. L., and P. R. Grant. 1987. Oscillating selection on Darwin's finches. *Nature* **327**:511–513.
- Grant, B. R., and P. R. Grant. 1989. Natural selection in a population of Darwin's finches. *American Naturalist* **133**:377–393.
- Grant, B. R., and P. R. Grant. 1993. Evolution of Darwin's finches caused by a rare climatic event. *Proceedings of the Royal Society of London*, **B 251**:111–117.
- Grant, P. R. 1986. *Ecology and evolution of Darwin's finches*. Princeton University Press, Princeton, New Jersey, USA.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.
- Huey, R. B., and A. F. Bennett. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* **41**:1098–1115.
- Hyatt, K. D. 1979. Feeding strategy. Pages 71–119 in W. S. Hoar, D. J. Randall, and J. R. Brett, editors. *Fish physiology*. Volume 8. Academic Press, New York, New York, USA.
- Jordan, N. 1991. Multivariate analysis of selection in experimental populations derived from hybridization of two

- ecotypes of the annual plant *Diodia teres* W. (Rubiaceae). *Evolution* **45**:1760–1772.
- Lack, D. 1947. Darwin's finches. Cambridge University Press, Cambridge, UK.
- Larson, G. 1976. Social behaviour and feeding ability of two phenotypes of *Gasterosteus aculeatus* in relation to their spatial and trophic segregation in a temperate lake. *Canadian Journal of Zoology* **54**:107–121.
- Lavin, P. A., and J. D. McPhail. 1986. Adaptive divergence of trophic phenotype among freshwater populations of the threespine stickleback (*Gasterosteus aculeatus*). *Canadian Journal of Fisheries and Aquatic Sciences* **43**:2455–2463.
- Losos, J. B. 1990. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**:1189–1203.
- Malmquist, H. J. 1992. Phenotypic-specific feeding behaviour of two arctic charr *Salvelinus alpinus* morphs. *Oecologia* **92**:354–361.
- Mayr, E. 1963. Animal species and evolution. Belknap, Cambridge, Massachusetts, USA.
- McPhail, J. D. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): morphological and genetic evidence for a species pair in Enos Lake, British Columbia. *Canadian Journal of Zoology* **62**:1402–1408.
- . 1992. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): evidence for a species pair in Paxton Lake, Texada Island, British Columbia. *Canadian Journal of Zoology* **70**:361–369.
- . 1993. Speciation and the evolution of reproductive isolation in the sticklebacks (*Gasterosteus*) of southwestern British Columbia. Pages 399–437 in M. A. Bell and S. A. Foster, editors. *Evolutionary biology of the threespine stickleback*. Oxford University Press, Oxford, UK.
- Norton, S. F. 1991. Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. *Ecology* **72**:1807–1819.
- Pashley, D. P. 1988. Quantitative genetics, development, and physiological adaptation in host strains of fall armyworm. *Evolution* **42**:93–102.
- Rauscher, M. D. 1984a. Tradeoffs in performance on different hosts: evidence from within- and between-site variation in the beetle *Deloyala guttata*. *Evolution* **38**:582–595.
- . 1984b. The evolution of habitat preference in subdivided populations. *Evolution* **38**:596–608.
- Richman, A. D., and T. Price. 1992. Evolution of ecological differences in the Old World leaf warblers. *Nature* **355**:817–821.
- Robinson, B. W., and D. S. Wilson. 1994. Character release and displacement in fishes: a neglected literature. *American Naturalist*, in press.
- Sanderson, S. L., J. J. Cech, and M. R. Patterson. 1991. Fluid dynamics in suspension-feeding blackfish. *Science* **252**:1346–1348.
- Schluter, D. 1993. Adaptive radiation in sticklebacks: size, shape and habitat use efficiency. *Ecology* **74**:699–709.
- Schluter, D., and P. R. Grant. 1984. Determinants of morphological patterns in communities of Darwin's finches. *American Naturalist* **123**:175–196.
- Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. *American Naturalist* **140**:85–108.
- Schluter, D., and J. D. McPhail. 1993. Character displacement and replicate adaptive radiation. *Trends in Ecology and Evolution* **6**:197–200.
- Schluter, D., T. D. Price, and P. R. Grant. 1985. Ecological character displacement in Darwin's finches. *Science* **227**:1056–1059.
- Schultz, E. T., L. M. Clifton, and R. R. Warner. 1991. Energetic constraints and size-based tactics: the adaptive significance of breeding-schedule variation in a marine fish (Embiotocidae: *Micrometrus minimus*). *American Naturalist* **138**:1408–1430.
- Shuter, B. J., and J. R. Post. 1990. Climate, population variability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* **119**:314–336.
- Sinervo, B., and J. B. Losos. 1991. Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology* **72**:1225–1233.
- Smith, T. B. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. *Nature* **329**:717–719.
- Taper, M. L., and T. J. Case. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology* **66**:355–371.
- Trexler, J. C., J. Travis, and M. McManus. 1992. Effects of habitat and body size on mortality rates of *Poecilia latipinna*. *Ecology* **73**:2224–2236.
- Via, S. 1991. The genetic structure of host plant adaptation in a spatial patchwork: demographic variability among reciprocally transplanted pea aphid clones. *Evolution* **45**:827–852.
- Wilson, D. S. 1989. The diversification of single gene pools by density- and frequency-dependent selection. Pages 366–385 in D. Otte and J. A. Endler, editors. *Speciation and its consequences*. Sinauer, Sunderland, Massachusetts, USA.