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Complex foraging polymorphism in bluegill sunfish

(osteichthyes: Centrarchidae/behavior/morphology/intraspecific variation)

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ABSTRACT **The bluegill sunfish (*Lepomis macrochirus*) is considered a generalist predator, adept at feeding in both the littoral and open-water habitats of North American freshwater lakes. We demonstrate adaptive intraspecific variation in morphology and foraging behaviors within single lakes. This variation appears to make individual fish specialized for feeding in either the littoral or open-water habitat. Discovery of a complex polymorphism in such a well-studied species suggests that adaptive variation may be more common than is currently perceived.**

Ecologists have long appreciated the fact that differences in morphology and behavior between species can be important in promoting coexistence, often through partitioning of resources (1). Less appreciated is the fact that differences among individuals within single species' populations can be just as great as the differences between species and can have similar ecological consequences (1, 2). There are several well-documented examples of adaptive intraspecific variation in foraging behavior and morphology (3, 4) as well as mimicry (5) and reproductive strategies (6), but the degree and frequency of functional diversification within species is unknown.

In this report, we present evidence for a complex foraging polymorphism involving multiple behavioral and morphological traits in bluegill sunfish (Centrarchidae: *Lepomis macrochirus*). Bluegill are often the most common fish species inhabiting the lakes and ponds of eastern North America and they have been studied extensively from the standpoint of foraging ecology (7), functional morphology (8, 9), mating behavior (6), and genetic diversity (10). They are considered a generalist predator, with a morphology adept at foraging either in open water for zooplankton or in the littoral zone for invertebrates that live among the sediments and aquatic vegetation. These two habitats differ substantially in the behaviors required for successful foraging (11), and bluegill are able to modify their foraging behaviors to some extent when they switch between habitats (11). Superimposed upon this flexibility, however, we show that individual bluegill possess a degree of inflexible behavioral and morphological specialization to the open-water or littoral habitats.

Behavioral Polymorphism

Bluegill search visually for prey while hovering motionless, using their pectoral fins to maintain their position in the water. If no prey item is detected during the hover, they move to another location and again hover. If a fish stops hovering prematurely, it risks not detecting cryptic prey, but by hovering too long it risks wasting time searching a location where prey are absent. Open-water and littoral zone habitats require different hover durations and patterns of movement for successful foraging. For example, open-water zooplankton eaten by bluegill (e.g., *Daphnia pulex*) are relatively conspicuous and unable to evade attack. As such, they can be searched for by short hovers with rapid movement between hovers. In contrast, vegetation prey (such as damselfly larvae clinging to vegetation or tube-dwelling chironomid larvae) can make themselves more cryptic by becoming motionless, hiding behind stems or withdrawing into the sediments if they detect the presence of a predator (12), so searching requires longer hover durations and more stealth. Thus, the best hover duration changes with prey type, prey density, and habitat structure. Patterns of movement between hovers also have important consequences for foraging success (11).

Previous studies showed that individual bluegill learn the searching techniques appropriate for each habitat, although they typically require a period of 3–5 days to reach a maximum asymptote in capture efficiency (11). Individuals differed, however, in the pattern and degree of their flexibility. To characterize these individual differences, laboratory foraging trials were conducted with bluegill collected from Warner Lake, a small (26-hectare) hard-water lake in southwestern Michigan. Each fish was placed in both vegetation and open-water environments for 18 feeding trials (see legend to Fig. 1), after which average feeding rates and hover durations were measured. The data presented here are from the final 6 trials for each prey type—after fish had reached asymptotic performance levels for each prey type.

The relationship between the hover durations used by individuals and their foraging rate during trials is presented in Fig. 1*A*. When feeding in the open water, bluegill that used shorter hover durations were more successful relative to fish that hovered longer. Conversely, individuals that used longer hover durations fed more effectively in the vegetation.

Individual bluegill used different hover durations in each habitat. Fig. 1*B* shows the mean hover duration used by individual fish when searching in the vegetation plotted against the hover duration they used when searching in the open water. The fact that points lie above the diagonal indicates that most fish were flexible and increased their hover durations in the vegetation habitat. The fact that the points fall into two clusters indicates a degree of inflexibility, with two relatively distinct behavioral types, especially when searching in the vegetation.

To test the stability of these differences, the same fish were held for 20 weeks (see Fig. 1 for holding conditions) and the experiment was replicated. The hover duration of an individual during the first experiment was an excellent predictor of its hover duration during the second experiment ($r^2 = 0.91$; $P < 0.01$ for open water; $r^2 = 0.83$; $P < 0.01$ for vegetation). Finally, similar patterns of individual variation in hover duration were detected in separate years with two different cohorts from Warner Lake (11). We have no direct evidence for a genetic component of these differences, but they are stable and repeatable and cannot be attributed to short-term feeding experience.

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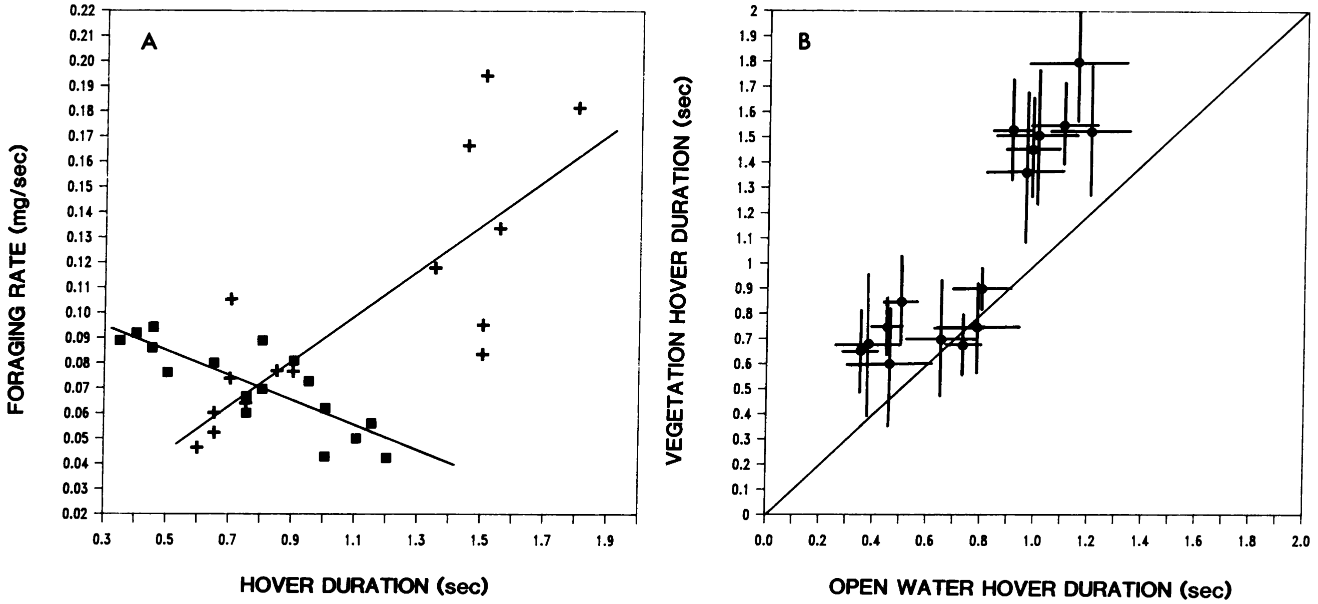

FIG. 1. *(A)* Foraging rates (mg dry weight per sec) for individual bluegill as a function of their hover durations used (mean of 6 feeding trials per fish). ■, Relationship for trials feeding on *Daphnia* in the open-water habitat ($Y = 0.11 - 0.05 \times X$, $R^2 = 0.71$, $P < 0.01$); +, relationship for trials feeding on nymphs in the vegetation habitat ($Y = 0.09 \times X$, $R^2 = 0.65$, $P < 0.01$). *(B)* Hover durations used by individual bluegill when searching for nymphs in the vegetation and when searching for *Daphnia* in the open-water habitat of aquaria. Each point represents the mean time (±1 SEM) of 6 feeding trials for a given fish in each habitat. Diagonal is line of equal hover duration in each habitat. Bluegill (standard length, 65 mm) were held in laboratory aquaria and fed a standard diet of commercial fish food for 8 weeks prior to the start of the experiments. Feeding trials were conducted in 160-liter aquaria (0.8 × 0.8 × 0.25 m) divided equally into vegetation and open-water habitats. The vegetation habitat contained nylon fabric aquarium plants similar in structure to *Potomogeton crispus* at a density of 180 stems per m^2. Individual bluegill ($n = 16$) fed on 2.2-mm *Daphnia pulex* (density, 0.25 per liter) in the open-water habitat for 18 sequential trials and were fed 5.0-mm damselfly nymphs (Coenagrionidae; density 31 per m^2) in the vegetation habitat for another 18 trials. Trials were videotaped for slow-motion analysis and lasted for 5 min or until all prey were eaten. Measurements were determined for each trial for each fish using captures until half the prey were eaten. Presentation order of prey types was randomized with half the fish feeding first in vegetation and then switched to the open water. Bluegill require more trials to reach maximum feeding rates in vegetation compared to open water (11), but there was no effect of presentation order on the asymptotic values for either capture rates or hover durations.

Differences in hover durations also correlated with the propensity of individuals to sample other habitats. The same fish were fed artificial food for 1 week, followed by an additional 6 feeding trials (as described above), with the exception that nymphs were present in the vegetation and *Daphnia* were present in the open water simultaneously. During these feeding trials, each hover "type" (corresponding to the two clusters in Fig. 1*B*) persisted longest in searching the habitat in which their foraging rate was greatest (Table 1). As a result, they spent most of their time in their "best" habitat and made very few visits to sample the other habitat.

Morphological Polymorphism

Fish species that are specialized for living in structurally complex habitats have a characteristic body plan that includes a deep and laterally compressed body, laterally inserted pectoral fins, and extended anal and dorsal fins, well suited for slow and precise maneuverability (9, 13). By contrast, fish species that dwell exclusively in the open water have more fusiform bodies that minimize drag and allow for efficient cruising while searching for widely dispersed prey (13). As a species that utilizes both habitats, bluegill have a body plan intermediate between these two extremes although more closely resembling the maneuverer form (13). If functional specialization exists within single populations, however, we might expect to find morphological types within a given lake that are relatively well adapted to single habitats.

Table 1. Mean persistence in searching habitats of short-hover and long-hover type bluegills when nymphs and *Daphnia* were available in aquaria simultaneously

Habitat	Short-hover type	Long-hover type
Open water	5.50 (1.97)	1.45 (1.38)
Vegetation	0.37 (1.41)	9.42 (2.66)

Classification of hover type corresponds to clusters in Fig. 1*B*. Persistence (sec ± 95% CI) is an index of giving-up-time in a habitat (equal to the time a fish searched unsuccessfully in a habitat before it stopped searching and moved into the other habitat minus the average time required to locate a prey item in that habitat).

To examine this possibility, a total of 212 fish were angled from both habitats on five dates between June 8 and October 11, 1986, from Holcomb Lake, a lake located near and physically similar to Warner Lake. The fish were photographed and nine measurements relating to fin size, fin placement, and general body proportions were calculated. Since habitat selection by bluegill is known to be influenced by the presence of predators, with smaller fish favoring the "safer" vegetation habitat over the open-water habitat (14), we restricted our analysis to fish of >8.0 cm standard length—large enough to be unconstrained by predation risk (14). Of these fish, there was no difference between habitats in mean standard length [open water, 9.11 ± 0.14 cm (SEM); $N = 122$; vegetation, 8.96 ± 0.12 cm (SEM); $N = 90$].

Significant differences in fin lengths, body proportions, and fin placements emerged between habitats, using analysis of covariance with standard length as the covariate to adjust for differences in fish size within habitats (Table 2; example in Fig. 2). Fish sampled from the vegetation had deeper bodies, longer pelvic and pectoral fins, and pectoral fins attached in a more posterior position compared to fish sampled from the open water. These differences appear adaptive as locomotor specializations to the two habitats,

Table 2. Differences in adjusted means (mm) of morphological measurements between fish caught in the vegetation and fish caught in the open-water habitats of Holcomb Lake

	Body	Fin length		Horizontal position	
	depth	Pelvic	Pectoral	pectoral fin	*n*
June 28, 1986	2.13*	0.33	1.27	0.76	33
July 7, 1986	0.75	0.74*	0.56	1.05*	35
Aug. 29, 1986	1.56*	1.60†	2.58†	1.21	38
Sept. 9, 1986	1.41†	0.42	0.94	0.61*	64
Oct. 11, 1986	1.49*	0.31	2.37‡	2.01‡	42
All dates	1.11‡	0.76‡	0.88†	0.98§	212

Means and significance levels were determined by analysis of covariance of single morphological measures with standard length as the covariate. Data are presented for each sampling date and are pooled for all dates. Note all differences are positive. Slopes of regression lines are not different between habitats.
*$P < 0.05$; †$P < 0.01$; ‡$P < 0.001$; §$P < 0.0001$.

with some fish better suited morphologically for the vegetation and others better suited to the open water (13). These types segregate into their appropriate habitats with some dates showing greater differences than others but with all dates showing the same pattern.

Although we have used differences between fish captured in two habitats to designate morphological types, this does not mean that the fish population is actually divided into morphologically distinct forms. In fact, distributions of single morphological characters tend to be unimodal when fish from both habitats are combined. However, when depth, fin sizes, and fin placement were combined in a canonical discriminant analysis, there was a significant difference between habitats and the distribution for the population along canonical axis tended to be bimodal (Fig. 3). This is, at best, only suggestive of bimodality in the population, since we cannot be certain that our sample contained fish from each habitat in proportion to their abundance in the lake.

These habitat-linked morphological differences do not appear to be the result of age differences or sexual dimorphism. Forty fish were selected randomly, half with positive canonical scores (vegetation types) and half with negative canonical scores (open-water types). Sex was determined by dissection and age was determined by counting annuli from scales. Each type had a similar sexual composition (60% males for open water, 70% males for vegetation; $G_{\text{adj}} = 0.11$, $P > 0.50$) and were of similar age [mean ages: 4.23 ± 0.57 yr (SEM) for open water and 4.42 ± 0.35 yr (SEM) for vegetation]. This does not mean that there is no sexual dimorphism in the population (since we did not look for this explicitly) but rather indicates that habitat-linked morphological differences are not attributable to differences in habitat choice by males and females.

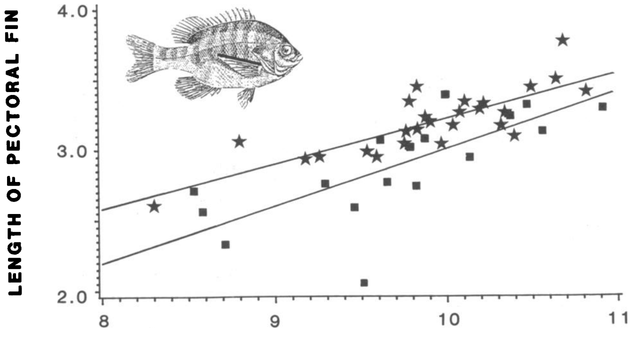

FIG. 2. Regression between the length of the pectoral fin and standard length for bluegill caught in the open water (■) and vegetation (★) habitats of Holcomb Lake on October 11, 1986. Adjusted means are different at $P < 0.001$ by analysis of covariance.

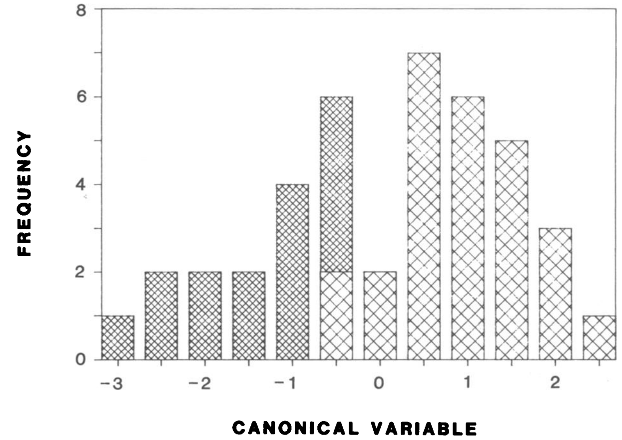

FIG. 3. Frequency distribution of the morphological canonical variable for fish caught on October 11, 1986. Heavy and light shading indicate fish caught in the open-water and vegetation habitats, respectively. (Standardized canonical coefficients: 0.41 × depth, 1.02 × pectoral fin length, 0.59 × horizontal position pectoral fin, 1.17 × pelvic fin length, −0.60 × vertical position of pectoral fin; $P < 0.0001$ for difference between habitats.) Canonical discriminant analysis was done by using the SAS CANDISC procedure (SAS Institute, Cary, NC, 1985). A single regression line was determined for each morphological measure vs. standard length. The canonical analysis was then performed on the residuals from these regressions for the entire data set and for each date independently. The discriminant function was significant using Wilks' λ for the pooled data ($P < 0.0001$) and for each date separately ($P < 0.01$) except for June 28, 1986 ($P = 0.16$).

Although the differences between habitats in single morphological characters are small (Table 2), they are correlated strongly with foraging success. A subset of bluegill collected on October 11, 1986 (six from each habitat) were photographed, measured, and retained for laboratory feeding trials (T.J.E., D.S.W., and K. Judy, unpublished data). These experiments showed a clear positive relationship between individuals's maximum foraging rates in the vegetation and their morphological canonical scores (Fig. 4). The expected negative correlation between canonical scores and open-water foraging success was less pronounced ($r^2 = -0.247$, $P > 0.05$), although perhaps the advantages of an open-water morphology (e.g., more efficient cruising) are less likely to be realized in the confined spaces of laboratory aquaria.

Correlations Between Behavior and Morphology

So far we have shown that both morphological and behavioral variation contribute separately to differences in habitat-specific feeding efficiency. If functional diversification exists within single lakes, however, we might also expect behavioral and morphological differences to correlate with each other. Two lines of evidence indicate that is the case.

First, differences in hover durations measured for fish from Holcomb Lake were directly correlated with morphological variation (Fig. 5); i.e., fish with a "vegetation morphology" used longer hover durations than fish with an "open-water morphology." Second, 12 fish retained from the Warner Lake behavioral trials were measured and classified as either open-water or vegetation types by using the discriminant function obtained for fish from Holcomb Lake. All 5 long-hover behavioral types were classified as vegetation morphological types, and 5 of 7 short-hover behavioral types were classified as open-water morphological types ($P = 0.028$, Fisher's exact test, two-tailed).

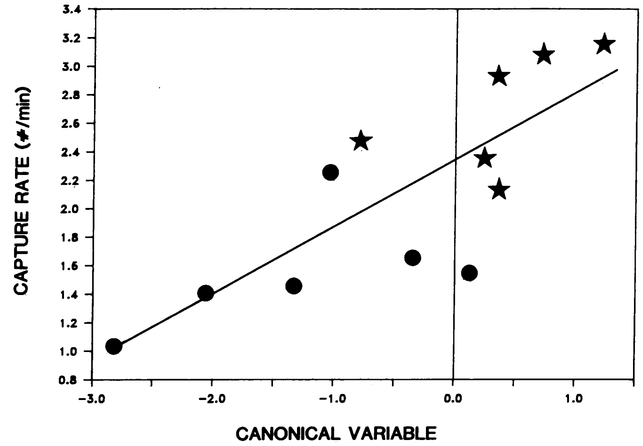

FIG. 4. Capture rates for fish from Holcomb Lake plotted against their morphological canonical scores. Experiments were conducted in 109-liter aquaria with *Simocephalus* (a littoral cladoceran that attaches itself to vegetation) density of 0.09 per liter and a vegetation stem density of 200 per m^2. Points are means for individual fish (mean of 6 trials following 12 training trials). ●, Fish that were caught in the open-water habitat; ★, fish caught in the vegetation habitat ($Y = 2.35 + 0.47 \times X$, $R^2 = 0.79$, $P < 0.05$).

Discussion

Our research suggests that the bluegill populations of Warner and Holcomb Lakes have functionally diversified into forms that are specialized to forage in the open water and vegetation. Our data specifically support four conclusions: First, bluegill adjust their searching tactics in ways that increase their foraging rates, but differences between individuals are stable and in some cases tend to cluster into behavioral types that can be interpreted as habitat-specific adaptations. Second, samples of bluegill captured from open-water and littoral zones are morphologically different from each other in ways that can be interpreted functionally. This does not mean that individual fish never switch between habitats (7), only that morphological variants tend to be found in the habitat to which they are best adapted. Third, morphological and behavioral variation have important consequences for foraging success, as measured in laboratory feeding trials. Fourth, morphological and behavioral variation are correlated with each other.

The study of resource partitioning has been motivated historically by questions of interspecific competition and its role in promoting the coexistence of closely related species, with some attention given to the role of niche diversification by age, sex, and size as ways of reducing intraspecific competition (see ref. 15 for recent review). The "niche-variation hypothesis" (16) explicitly acknowledges the importance of both within- and between-individual components of phenotypic variation, predicting increased differences between individuals when interspecific competition is low. It is interesting to note that a major resource competitor with bluegill, the pumpkinseed sunfish (*Lepomis gibbosus*) (17), is rare in Holcomb Lake (unpublished observation) compared to other local lakes (18). This fact alone might suggest that bluegill are becoming functionally diversified to reduce intraspecific competition (a true test would require comparisons of lakes differing in the relative densities of bluegill and pumpkinseed). However, the scenario we are presenting differs from the niche-variation hypothesis in at least one important way; that there is directed adaptive divergence into different habitats rather than a simple across-the-board increase in between-individual variation to reduce intraspecific competition.

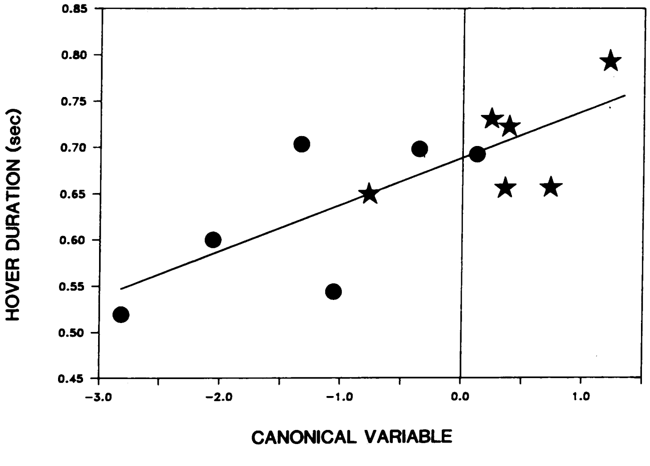

FIG. 5. Hover durations for fish from Holcomb Lake plotted against their morphological canonical scores (see legend of Fig. 4 for details) ($Y = 0.69 + 0.50 \times X$, $R^2 = 0.57$, $P < 0.05$).

Adaptive variation can be created in several ways and does not imply the existence of underlying genetic variation. Examples of environmental induction of variation in bone morphology during development are well known for fishes (19, 20). This induction, however, involves a direct exposure of the phenotype to two environments to produce the phenotypic variation. By contrast, the bluegill foraging polymorphism develops in a single habitat, since bluegill smaller than 7.5 cm standard length are confined to the littoral zone to avoid predation by largemouth bass (14). Indeed, Layzer and Clady (21) have shown that young-of-year bluegill trapped at various water depths in the littoral zone show a pattern of morphological differences by depth similar to what we have described between habitats. This indicates that differences develop early in life, suggesting that underlying genetic variation is plausible, although it obviously must be demonstrated.

Behavioral variation is well known for many species (22, 23), including the feeding behavior of birds (24) and fishes (25, 26). Frequently, however, behavioral differences are thought to be temporally labile and most likely the result of individual learning. Our results suggest that the notion of behavioral flexibility within individuals must be supplemented by a notion of behavioral inflexibility between individuals. Indeed, both notions are contained in the concept of learning programs (27), in which organisms are selected to perceive and respond to certain kinds of information. This is especially implicit in the study of "rules-of-thumb" in the optimal-foraging literature, where organisms use simple decision rules as short cuts that only approximate optimal behavior (28, 29). If learning programs actually govern behavioral flexibility, then the programs themselves might vary adaptively within single populations (23).

Uncovering the basis for the correlation between morphology and behavior is an interesting area for future research, touching on many areas of evolutionary ecology. The dramatic differences in searching persistence within habitats (Table 1) suggest that individual bluegill used different criteria when making decisions about where to forage. However, it is equally plausible that individuals used the same decision criterion (e.g., feed where you get the most energy gain per time) and simply learned to go where they foraged most profitably (11). In the latter case, morphological variation is responsible for the differences in habitat choice by directly influencing how well an individual can feed within a habitat. Indeed, computer simulations show that continuous variation among individuals in feeding efficiencies can result in populations becoming split between habitats even when all fish use the same decision rule (23).

It will be interesting to know how this foraging polymorphism interacts with the well-studied polymorphism in male bluegill mating tactics (6, 30) A cuckolding male type matures sexually at a small size and parasitizes the nests of large territory-holding males. Although the role of development in producing this polymorphism is not well known, a definite genetic component has been demonstrated (M. Gross and D. Philipp, personal communication).

According to theoretical models, the evolution of adaptive polymorphisms requires density- and frequency-dependent selection (31, 32). Fitness associated with an activity must decline as the numbers engaged in the activity increase, which makes it advantageous to engage in alternative activities (33). Density- and frequency-dependent selection are easy to envision for the male-mating polymorphism, because the morphs interact directly with each other. The foraging morphs are more likely to influence each other indirectly through their effects on the various prey populations. Bluegill are well known to compete for resources in the littoral zone (17, 34), so the idea of density- and frequency-dependent selection on bluegill mediated indirectly through prey depletion is plausible.

The concept of functional diversity within single gene pools has a long history in evolutionary thought, but few empirical examples are known and many theorists regard it as an unlikely possibility (35). The existence of a complex foraging polymorphism in a species as well studied as the bluegill sunfish suggests that functional diversity must be specifically looked for to be found and may be far more common in nature than currently perceived.

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