The increase in lactate production presumably represents increased ATP production by the glycolytic pathway in the absence of optimal oxidative phosphorylation (Pasteur effect). Failure of lactate production to return to control values has not been explained in this system. There is evidence suggesting uncoupling of oxidative phosphorylation as a result of brain edema (*14*). This implies oxygen consumption without ATP production and thus an ongoing requirement for glycolytic ATP. Increased lactate production due to intracellular edema has been reported in an intact organ system. Young (*15*) produced edema in the isolated perfused rat lung by increasing pulmonary capillary pressure and by altering alveolar epithelial permeability. Intra-alveolar epithelial edema was present with both pathogenetic mechanisms. Pulmonary edema in this system was associated with increased total lung lactate production. When the lungs were filled with isosmotic NaCl (so that no intracellular edema was present), no increase in lactate production occurred (*15*).

Cellular dehydration appears to produce marked alteration of oxygen utilization. The Pasteur effect was absent, reflecting another aspect of altered metabolic control associated with cellular injury. The reduced $\dot{Q}O_2$ has been reported in isolated mitochondria. Increasing the concentration of mannitol and sucrose in the incubating medium reduces $\dot{Q}O_2$, although this can be reversed in this preparation by adding permeant ions to restore the normal water content of the matrix (*13*).

These studies suggest that regulation of intracellular and subcellular water activity is required for normal cellular energy metabolism. The reversible nature of the changes produced by intracellular edema helps to explain the beneficial effects of administering a nonionic osmotic agent such as mannitol in the treatment of certain disorders associated with cellular swelling. Changes associated with cellular dehydration are profound and in this cell system cannot be reversed.

NORMAN J. LEWISTON
JAMES THEODORE
EUGENE D. ROBIN
Departments of Pediatrics and *Medicine, Stanford University School of Medicine, Stanford, California 94305*

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Niche Shifts in Sunfishes: Experimental Evidence and Significance

Abstract. *Three species of sunfishes segregate ecologically when stocked together in small ponds. When each species is stocked separately in replicate ponds, it exhibits competitive release through increases in growth rate and average food size. Niche shifts are indicated by convergence of these species to the same food habits in the absence of competitors. These shifts are due to phenotypic (behavioral) plasticity. The significance of niche flexibility is related to seasonal patterns in resource availability.*

The premise that animal communities are shaped primarily by competition serves as a cornerstone of much recent ecological theory (*1*). Morphological changes (character displacement) and ecological changes (niche shifts) occurring in species when the complement of closely related species differs are generally considered the strongest evidence supporting this premise (*2*). The forms and magnitudes of these changes also indicate critical niche dimensions and mechanisms of ecological segregation.

Niche shifts can arise from both genetic changes and phenotypic (behavioral) plasticity (*3*). The latter potentially enables a species to alter its ecology immediately upon removal of a competitor (or competitors). Although data of this sort bear on the development of a theory of community structure (*2, 3*), very little is known about how species differ in these two components of niche flexibility.

Niche shifts are most often revealed when populations of a species inhabiting presumably saturated mainland and depauperate island communities are compared. In the absence of competitors species often increase in abundance or expand the range of habitats, foraging heights, altitudes, or food utilized (*1, 4*). In such comparative studies, however, separating the effects of competition from the effects of relative availabilities of habitats and foods is a major operational problem (*2*). In addition, it is difficult to separate the genetic and phenotypic components of the observed niche shift. Both of these problems can be minimized by removing or adding species to communities in replicate environments and comparing resource utilization. The availability of food and habitat types will be similar and therefore less likely to confound the results. If the experiment is performed over a short time period and reproduction is precluded, any response by a species can be attributed to phenotypic plasticity.

We report a set of experiments designed to examine niche shifts in three species of freshwater sunfishes (Centrarchidae): the bluegill (*Lepomis macrochirus*), pumpkinseed (*L. gibbosus*), and green sunfish (*L. cyanellus*). These species coexist in the littoral zone of small lakes over a broad region of central North America and attain about the same adult body size (150 to 300 g). Data from natural lakes indicate that the green sunfish inhabits regions closer to the shore and in shallower water than the other two species. The bluegill and pumpkinseed are more widely distributed in the littoral; the former predominantly inhabits the water column while the latter remains near the bottom (*5*).

The experimental facility consists of 18 identical circular ponds, 29 m in diameter and 1.8 m deep, located at the Kellogg Biological Station of Michigan State University. Each pond contained a stand of cattails (*Typha* spp.) extending 2 m from shore. Apart from this area, there were patches of submergent vegetation (*Chara* and *Potomogeton* spp.), growing to within 0.5 m of the surface; between these patches were areas of exposed sediments.

Four ponds were selected for uniformity of these characteristics. In one pond, 900 individuals of each species were stocked together (2700 total); in the remaining three, 900 individuals of each species were stocked alone (*6*). Mean size of the individuals of each species ranged from 26 to 28 mm in length ($N > 100$ for each species). These fish were spawned the previous year in local brood ponds. The experiments were initiated in June 1973 and terminated by draining the ponds in October 1973.

At intervals from 3 days to 2 weeks during the experiment, 15 individuals of each species were seined for stomach analyses and growth rates. Over 950 stomachs were examined, and the contents were identified to the lowest taxonomic level possible (40 categories; more than 50 percent to genus or species). The contents of each stomach were counted, and the intact prey were measured. Length-weight regressions were determined for each prey category, permitting conversion of the counts to weights.

Mortality was consistent within species: 12 percent when stocked together and 12 percent when stocked separately for the bluegill; 7 percent and 3 percent for the pumpkinseed, and 16 percent and 17 percent for the green. Because so few fish reached sexual maturity during the experiment, reproduction was insignificant. Thus the growth rates are not confounded by reproduction or mortality. Since growth rate can be considered commensurate with fitness (*7*), relative growth is an index of the ecological consequences of the observed niche shifts. Growth thus provides a convenient measure of changes in fitness that in most other organisms can be assessed only by direct, long-term demographic observations.

The average initial and final individual dry weights of each species are shown in Table 1. Release from interspecific competition is manifested by increased growth of each species in isolation. The magnitudes of this response, however, differ. The bluegill shows an increase of 179 percent in mean size when alone; the green, 30 percent; and the pumpkinseed, 14 percent.

Food habits indicate the nature of the niche shifts. Three prey categories were assigned on the basis of life form: (i) prey restricted to the stems or leaves of vegetation (for example, *Simocephalus*, Coenagrionidae), (ii) zooplankton found in the open water column (for example, *Bosmina*, *Cyclops*), and (iii) the epi- or infauna of the sediments (for example, Chironominae, *Caenis*). These prey groups are, in general, spatially discrete and require different foraging strategies and feeding morphology. A fourth, residual category contains those prey which are not specific to one of these habitats. The first three food categories discriminate habitat use since food and habitat use are coextensive, that is, collapse into a single niche dimension. Although the fourth category represents an appreciable proportion of the diets of these fish, we assume that these prey are foraged according to the patterns of habitat use as determined by the first three categories. Direct observations on habitat use tend to support this contention (*5*).

When species are stocked separately, the resource utilization patterns are similar. Prey from the vegetation comprise 61, 41, and 43 percent of the diets (by dry weight over the season) of the bluegill, pumpkinseed, and green, respectively (Table 2). When stocked with congeners, the diet of the green sunfish changes very little, but the diets of the bluegill and pumpkinseed shift (Table 2). The bluegill concentrates on prey from the open water column, whereas the pumpkinseed feeds largely on prey associated with the sediments. Thus considerable ecological segregation occurs when congeners are present.

Current theory of optimal resource utilization may be used to interpret our results. An optimal resource set is determined by adding habitat patches (foods) to the foraging itinerary (diet) according to a utility ranking (that is, return per unit effort) until some cost benefit function is minimized (*8*). In general, the utility of a prey increases with its size when prey are small relative to that of the predator (*8, 9*). Thus, habitats containing larger prey will offer greater return per unit effort, provided that prey abundance or availability does not greatly differ among habitats. In the ponds larger prey reside in the vegetation, and all species apparently maximize return by foraging in this habitat type. This contention is supported by three observations. (i) Average food size is largest in the green sunfish, which normally forages the vegetation (Table 3). (ii) Negligible niche shift is shown by the green sunfish when it is released from interspecific competition. (iii) Both the bluegill and pumpkinseed shift to utilizing this habitat in the absence of competitors. The relation between changes in growth and food size in the absence of competitors is another indication of the importance of food size. In all cases, release from interspecific competition is associated with an increase in average food size (Table 3). The magnitude of this increase is directly related to the magnitude of the growth response for each species (that is, percentage increases in weight and average food size when the fish were stocked separately relative to when together are 14 and 40 percent for the pumpkinseed, 30 and 46 percent for the green, and 179 and 202 percent for the bluegill).

Table 1. Mean size of individual *Lepomis* fish in October with mean values given in grams of dry weight ± standard error. The initial individual weight of each species was approximately 0.1 g ($N > 100$).

Fish	Species together	Species alone
L. macrochirus	1.29 ± 0.02	3.6 ± 0.15
L. gibbosus	1.21 ± 0.03	1.38 ± 0.04
L. cyanellus	1.34 ± 0.03	1.74 ± 0.04

Table 2. Percent contribution of prey categories to the diets of the bluegill (*L. macrochirus*), pumpkinseed (*L. gibbosus*), and green sunfish (*L. cyanellus*) on the basis of dry weight and computed for the entire experimental period.

Prey	*L. macrochirus*	*L. gibbosus*	*L. cyanellus*
	Species alone		
Vegetation dwellers	61	41	43
Benthic in- and epifauna	10	12	23
Open water zooplankton	8	1	1
Other	21	47	33
	Species together		
Vegetation dwellers	15	5	40
Benthic in- and epifauna	15	34	12
Open water zooplankton	33	6	4
Other	37	55	44

Table 3. Mean size of food (milligrams of dry weight ± standard error) computed for the entire experimental period.

Fish	Species together	Species alone
L. macrochirus	0.0065 ± 0.001	0.0196 ± 0.002
L. gibbosus	0.0277 ± 0.004	0.0388 ± 0.007
L. cyanellus	0.0404 ± 0.008	0.0590 ± 0.009

The addition of a competitor should not change the utility or ranking of prey types to a species (*1*). In a homogeneous environment, therefore, competitors will usually increase the range of items a species uses and will consequently exaggerate overlap in resource utilization. When the environment is composed of different habitat or patch types, however, the argument is changed in an important way. If the competitor concentrates its efforts in a given patch type, it can change the utility of that habitat to the species already present. This may alter the ranking of habitats such that a previously "preferred" habitat is now excluded from the foraging itinerary and niche separation on the habitat dimension occurs (*1*). In this system all species clearly prefer to forage the vegetation. With the green sunfish concentrating on this habitat, however, the other two species largely abandon this area and utilize, respectively, two different habitat types. We may visualize this as a case where the relative utilities of the remaining habitats are elevated differentially to these species owing to the decline in utility of the vegetation. This will occur if habitats differ sufficiently (for example, in food size or mechanisms required for prey extraction), so that very different behavioral or morphological adaptations are required to utilize them effectively. For these sunfish this appears to be an important mechanism permitting coexistence in multiple species arrays.

Examination of the functional morphology and behavior of these species supports this argument. The bluegill possesses long, fine gill rakers which retain small prey, whereas the pumpkinseed has very short, widely spaced gill rakers that are less effective in retaining small prey but do not foul when sifting organisms from sediments. The bluegill exhibits a greater tendency to school, while the pumpkinseed is more solitary and aggressive; in general, these adaptations are associated, respectively, with open water planktivores and benthic feeding fishes. Thus these two species opt for quite different habitat or prey types when competitive pressure lowers the utility of the vegetation foraging mode. We have evidence that the advantage of the green sunfish in the vegetation stems both from a greater foraging efficiency in this habitat and interference with the foraging of conspecifics. Whether the habitat ordering or segregation is hierarchical or not is not known because experiments with combinations of two species have not yet been performed.

These fish exhibit considerable phenotypic niche flexibility, a trait generally associated with those species inhabiting marginal environments and therefore frequent colonizers (*10*). We believe that the adaptive significance of plasticity in sunfishes is related to the seasonal patterns in resource availability. The food habits of fish in temperate lakes often converge during the spring flush in food levels; however, as resources decline through the summer and fall, these food habits diverge (*11*). The ability to shift to foraging patterns that maximize yield during periods of superabundant resources would be of obvious benefit. The increased segregation with decline in resources tends to support the foraging model invoked earlier.

We have demonstrated niche shifts related to the presence of congeneric sunfishes, an indication of the importance of competition in structuring this community. Furthermore, these niche shifts reveal the extent and potential significance of phenotypic niche flexibility. Species such as these, which possess considerable ecological flexibility, hold much promise for experimental study of mechanisms potentially important to the organization of communities.

EARL E. WERNER
DONALD J. HALL
W. K. Kellogg Biological Station
and Department of Zoology,
Michigan State University,
Hickory Corners 49060

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7. Fish exhibit indeterminate or plastic growth, and factors bearing on fitness are generally positively related to size, that is, fecundity [T. Bagenal, in *The Biological Basis of Freshwater Fish Production*, S. Gerking, Ed. (Wiley, New York, 1967), p. 89], dominance and growth potential [K. Onodera, *ibid.*, p. 345; T. Jenkins, *Anim. Behav. Monogr.* **2**, 57 (1969); R. Parker and P. Larkin, *J. Fish. Res. Board Can.* **16**, 721 (1959)], and survivorship [J. McFadden and E. Cooper, *Physiol. Zool.* **37**, 355 (1964)].
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Panhandling: Sharing of Resources

Abstract. *Panhandling was used to study sharing of resources. Male panhandlers were more successful in spring than in autumn. Female panhandlers were more successful than males in autumn. Panhandlers were generally successful only when submissively approaching individuals who were eating. Families and male-female pairs were resistant to panhandling. The results are discussed in terms of reciprocal altruism and kinship selection.*

Food sharing among nonhuman primates has been observed only in chimpanzees (*Pan troglodytes*) (*1*). Baboons (*Papio anubis*) sometimes tolerate the stealing of food (*2*). Submissive behaviors and begging gestures are essential displays. Food sharing between related chimpanzees, such as between mother and offspring or between siblings (*3*), and the portioning of captured prey among the hunters and other familiar conspecifics indicate that there are "rules-of-the-game" as well. These rules may be influenced by kinship selection (*4*) and reciprocal altruism (*5*). The evolution of sharing food with relatives could be mediated by kinship selection, with the sharing increasing the fitness of individuals with common genes. Sharing food with individuals who are not relatives but who could benefit the giver or his relatives could be an example of reciprocal altruism. Although the sharing of food and other resources is an established practice among humans (*6*), the important behaviors, contexts, and rules have not been studied in detail until now.

Panhandling is a social situation where a supposedly needy individual requests or begs for money from a potentially helpful stranger. Observations of several panhandlers indicated that sex, eye contact, postural stance, dress, weather, and the amount of money specifically requested may be important in successful panhandling. For our experiment we used several college students as panhandlers. The experiment was designed to answer four questions: (i) What combinations of individuals share with strangers, (ii) what characteristics of the panhandler facilitate sharing, (iii) what environmental aspects influence the process, and (iv) what per-

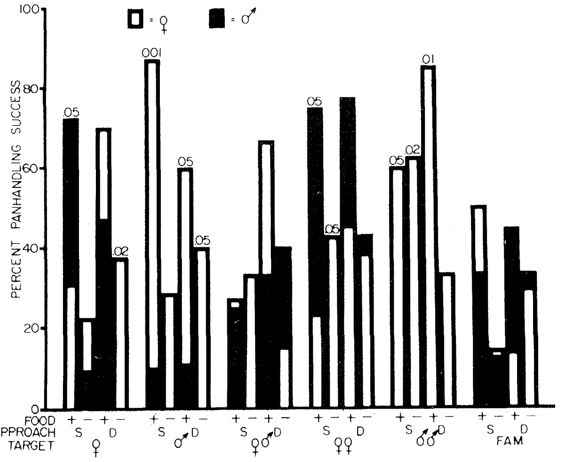

Fig. 1. Comparative success of female and male "panhandlers" individually approaching an approximately equal number of target groupings of (i) one or two females or males, (ii) a female and male together, (iii) a family with at least one child. Significant differences between male and female panhandlers, in terms of probabilities, are shown above the respective bars. Panhandlers approached either submissively (*S*) or dominantly (*D*) a target consuming food (+) or not (−); *FAM*, family.