Density and Competition Among Sunfish: Some Alternatives

Werner and Hall (*1*), in their report on the causal mechanism producing niche shifts in three congeneric sunfish, concluded that congeneric competitors induced shifts in habitat use since each species converged on the same pattern of habitat use when stocked singly in a pond; moreover, the shift to preferred habitats when alone led to consumption of larger prey items and increased body growth. Because of the paucity of relevant data presented, their conclusions are untenable.

A pond stocked with all three species had three times the number of fish as those stocked with a single species. The justification given for this experimental design was to control the amount of intraspecific competition within a habitat type, since habitat use was "fairly discrete"—a term not exactly described, so the validity of the justification cannot be assessed. Whether justified or not, the lack of control for total sunfish density produces a potential ambiguity in interpretation. Observed differences can be attributed either to the presence of other species (as Werner and Hall argue) or to that of other individuals regardless of species. With this flaw in experimental design, alternate explanations for the observed habitat shifts are as compatible with the data presented as that proposed by Werner and Hall.

Werner and Hall's explanation for the observed habitat shifts is based on an assumption that larger prey items are more efficiently used by the sunfish than are an equivalent total biomass of smaller prey items: Since the vegetation habitat contains the largest prey items, it is preferentially used by each species when stocked alone. The increase in larger prey available in the monospecific situations, because of shifts to the vegetation habitat, causes the observed increase in fish size.

To demonstrate that the increased growth in the fish is a result of the quality (mean biomass) of prey rather than of its quantity (total biomass), requires evidence that the quantity of prey consumed by the fish did not differ among treatments. By not presenting such evidence, Werner and Hall leave their results open to the alternate explanation that an increase in quantity of prey (a result of the lower total sunfish density) caused increased growth of the sunfish in the monospecific situations and that the increase in sunfish size resulted in an increase in mean prey size consumed. The differences among the three species in their growth increase, which can be explained by asymmetrical competitive interactions among the species, are compatible with either explanation for the increased growth of the sunfish.

Werner and Hall use the species composition of the diet as a measure of habitat use. Thus habitat shifts are concluded from changes in the species composition of the diet. However, they present the supporting data as percentage composition by weight rather than by number. A large increment in the percentage by weight of large prey items can result from a much smaller increment in the percentage by number. Since mean prey size varies among the habitats, a shift to the vegetation habitat, containing the largest prey, may be less dramatic than that indicated by their published results.

Werner and Hall do not dismiss potential explanations other than that associated with efficiency in feeding for the observed habitat shifts. To someone ignorant of the natural history of the fish, an explanation of the preference for the vegetation habitat based on escape from predators is as reasonable as that based on efficiency in feeding.

The system chosen by Werner and Hall is a potentially productive one because of the ease of experimental manipulation. However, many variables have not been adequately controlled, so that the conclusions are not supported by the evidence presented. Alternative explanations are as plausible as the one presented, although additional evidence may prove them false. The final conclusion, that the observed niche shifts indicate the importance of food resource competition in structuring this fish community, does not follow from this study. The fact that fish get larger when more food is available under the experimental conditions does not mean that food is a regulating resource for these fish and, therefore, what is competed for; egg-laying sites, cover, or something else may well be the primary factor regulating the density of their natural populations.

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References and Notes

1. E. E. Werner and D. J. Hall, *Science* **191**, 404 (1976).
2. I thank Leigh Van Valen for his comments.

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Maiorana's (*1*) alternatives are not consistent with our data and do not weaken our case for the mechanisms of habitat shifts in sunfishes. The questions we (*2*) asked were: (i) Are these species genetically fixed in their habitat utilization or are they phenotypically flexible? (ii) Is habitat use related to the presence of congeners and, if so, do niche shifts in the absence of congeners suggest the nature of the species interactions? Our experimental design was predicated on prior direct observations of habitat utilization by the three *Lepomis* species when stocked together at the densities used in the experiment. Extensive observations by divers showed that a single species accounted for more than 90 percent of the fish in a specified habitat. Furthermore, the habitat utilization of these species in natural lakes corresponds directly to that which we described in the ponds (*3*).

The physical nature of the habitats (for example, the vegetated shore zone, areas of exposed sediments, and the open water column) and the fact that distinct prey communities occupy such habitats is the basis for our conclusion that habitats and their use by the fish were "fairly discrete." Consequently the most appropriate design was to "remove" congeners and monitor niche shifts in the remaining species.

If the congeners were removed and the density of the remaining species were tripled to make equivalent densities in all ponds, then intraspecific competition would be potentially three times greater in the single-species ponds compared to the three-species ponds. Any interpretation of niche shifts would thereby be confounded by increased intraspecific competition within the species' habitat. Our design holds intraspecific competition constant but allows interspecific competition to vary. Other designs that would have allowed both forms of competition to vary can be imagined, but available resources and time did not permit us to attempt these.

Maiorana's (*1*) chief objection concerns our interpretation that, for reasons of foraging efficiency, the two species not utilizing the vegetation when together shifted to this habitat in the absence of congeners (primarily to utilize the larger food particles found there). Her alternative explanation is that decreased sunfish density in the monospecific situations resulted in more prey available and, therefore, greater growth; as a consequence of larger individual size, the fish then consumed larger food particles (presumably shifting to the vegetation to do this?). If this were the case then a positive relation between average food size and fish size should exist since all ponds were stocked with fish of identical size. However, there is either no relation (*L. cyanellus*) or a negative relation (*L. macrochirus* and *L. gibbosus*) between average food size and fish size in the monospecific situations. Fish actively select the larger food particles that are within their handling capabilities (*4*), and foraging efficiencies are the most compelling reason for this (*5*).

Maiorana states that the niche shifts may not be as dramatic as the data indicate because diet components were presented as percentage by weight rather than prey number. *Lepomis macrochirus* showed the most dramatic increase in food size because of its shift from the open water to the vegetation, and therefore any bias would be most evident here. We can compare the number of open water prey in the diet relative to the resource base since prey samples were obtained in each habitat every week (*6*). There is no statistical difference in the abundance of open water prey (that is, *Bosmina, Chydorus, Cyclops*, and *Daphnia*) in the two ponds containing *L. macrochirus*. Thus, if *L. macrochirus* spent the same proportion of time foraging in the open water in the two ponds they should obtain similar numbers of prey (in neither pond did stomach contents approach satiation levels which would affect foraging time). Date-by-date comparisons indicate that, on the average, the number of open water prey consumed by *L. macrochirus* when alone was only 9 percent of that consumed when with the congeners. In the case of *L. gibbosus* the shift based on an analysis of prey numbers is even clearer. Thus absolute numerical comparisons in reference to the resource base also indicate a striking shift, further strengthening our original argument.

More recent studies of the interactions among sunfish have supported our interpretation of the niche shifts. We have confined *L. macrochirus* and *L. cyanellus* alone and together at equivalent overall densities to large patches of the vegetation habitat. Under both conditions, *L. cyanellus* grew larger and consumed greater amounts of food and larger food sizes than *L. macrochirus*. This leads to an asymmetrical competitive effect of *L. cyanellus* on *L. macrochirus* in the vegetation (*7*). The magnitude of this effect is sufficient to cause *L. macrochirus* to shift to the open waters in the presence of *L. cyanellus* as we originally hypothesized.

Maiorana suggests that small fish may be associated with vegetation as a refuge from predators. Small *Lepomis* species are found primarily within 0.5 m of the vegetation cover in natural lakes (*3*). In our ponds patches of vegetation grew within 0.5 m of the surface (*2*). Thus cover should not limit access to the habitats preferred by these fish. Moreover, the predators that have access to the ponds (bullfrogs, herons) utilize the shallow shoreline regions dominated by *L. cyanellus*, the species that does not shift when congeners are removed.

We are aware that a number of factors remain uncontrolled in field experiments. The purpose of imposing control in any experiment is simply to increase confidence that a response can be attributed to a given factor. The experiment we presented represents an improvement in this direction over the "natural experiments" that ecologists often must rely on to obtain answers to the questions currently posed in community ecology.

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1. V. C. Maiorana, *Science* **195**, 94 (1977).
2. E. E. Werner and D. J. Hall, *ibid.* **191**, 404 (1976).
3. ______, D. Laughlin, D. Wagner, L. Wilsmann, F. Funk, *J. Fish. Res. Board Can.*, in press.
4. Most kinds of prey available in the ponds within the handling capabilities of the size fish we used [E. Werner, *ibid.* **31**, 1531 (1974)]; size/selection in fish has been discussed by J. Brooks [*Syst. Zool.* **17**, 273 (1968)], M. Galbraith [*Trans. Am. Fish. Soc.* **96**, 1 (1967)], and D. Hall, W. Cooper, E. Werner [*Limnol. Oceanogr.* **15**, 829 (1970)].
5. E. Werner and D. Hall, *Ecology* **55**, 1042 (1974); J. Paloheimo and L. Dickie, *J. Fish. Res. Board Can.* **23**, 1209 (1966).
6. E. Werner and D. Hall, unpublished data.
7. ______, in preparation.
8. We thank D. Beaver, P. Werner, and L. Wilsmann for comments.

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