

A FIELD TEST FOR COMPETITIVE INTERACTIONS
AMONG FORAGING STREAM FISHES

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A FIELD TEST FOR COMPETITIVE INTERACTIONS AMONG FORAGING STREAM FISHES.—Midwater stream fishes commonly segregate in the water column; that is, co-occurring species, although overlapping substantially, tend to differ in their mean vertical distance from the substrate (Mendelson, 1975; Baker and Ross, 1981; Gorman, 1988a). Water column fishes often cannot be differentiated on the basis of other variables describing habitat use and may, in fact, forage together in mixed-species groups (Moyle and Li, 1979). For this reason, several researchers have concluded that segregation in the water column promotes species coexistence (Mendelson, 1975; Baker and Ross, 1981; Gorman, 1988a). Vertical segregation could permit species to partition food resources, because species occurring near the substrate may feed on benthos, whereas species occurring farther from the substrate may feed on drifting prey from different levels of the water column. Conversely, Grossman et al. (1987) concluded that vertical segregation among five lotic cyprinid species was not a result of resource partitioning because most species fed on benthic prey. Clearly, the importance of vertical segregation to coexistence in stream fishes depends on the extent to which this phenomenon actually reduces interspecific competition.

Previous studies of competitive interactions among water column cyprinids have tested for shifts in midwater position by species in single-versus mixed-species groups. Allan (1986) and Gorman (1988b) tested for interactive segregation (*sensu* Brian, 1956) in the water column by cyprinids foraging in experimentally composed groups, i.e., in either a fluvium (Allan, 1986) or aquaria (Gorman, 1988b). Gorman (1988a) also tested for interactions between pairs of cyprinid species foraging in a stream by comparing the vertical distribution of each species in the presence and absence of heterospecifics. These studies provided evidence that minnows may adjust vertical distribution in response to individuals of other species; in fact, in all three studies, some species shifted toward each other rather than segregating. Thus, although there is evidence that interspecific differences in ver-

tical distribution may result from interactive segregation, under some conditions (e.g., intense predation), the advantages of group foraging may promote closer associations among foragers despite competitive pressures (Allan, 1986; Gorman, 1988a).

Our approach differs from previous studies in that we tested for competitive interactions among water column fishes, within an assemblage lacking strong patterns of vertical segregation. We previously found that the water column fishes inhabiting a study site in the southern Appalachian Mountains extensively overlapped in microhabitat use (Grossman and Freeman, 1987). Of six pairwise comparisons, we only found differences in vertical water column position between rosyside dace (*Clinostomus funduloides*) and one other cyprinid, the warpaint shiner (*Luxilus coccogenis*). In addition, rosyside dace, other cyprinids, and rainbow trout (*Oncorhynchus mykiss*) often foraged together in mixed-species groups. These observations prompted us to question the role of interspecific competition in the observed patterns of high overlap in microhabitat use and water column position. To test for competitive interactions in mixed-species foraging groups, we examined the effect of other species on the tendency of rosyside dace, the most abundant water column species in the assemblage, to forage in a particular location.

Observations in our study sites show that a group of fish foraging at a particular site varies in number of fish and species composition through time. This variation, which results from individual fish frequently moving among alternate foraging sites in a given stream reach, provides a mechanism for testing for avoidance (or attraction) among foragers. Specifically, one can examine the rates of fish movements in and out of a foraging site in relation to group composition at the site. If fish avoid foraging near each other, for example, then either the probability of arrivals should decrease, or departure probability should increase, with increasing group size. This approach is a modification of Caraco's (1979, 1980) method for measuring flocking tendency in birds. A separate analysis showed that interactions among rosyside dace are often minimal and that foraging groups frequently are the result of individuals independently aggregating at feeding sites (Freeman, 1990).

Here, we test for effects of other water column fishes on movements and foraging behavior of rosyside dace and discuss the potential for interspecific competition.

Study site and methods.—We worked in two streams, Coweeta Creek and Ball Creek, located at the Coweeta Hydrologic Laboratory (United States Department of Agriculture Forest Service, Macon County, North Carolina). Although the streams drain experimental watersheds (described in Swank and Crossley, 1987), stream segments used in this study flow through relatively undisturbed, mixed-hardwood forest. We used four study pools, located 40–190 m apart, that ranged from 9–16 m long, and from 3–6 m wide. The particular observation site used in a given pool on a given date depended on flow conditions and where groups of dace were foraging.

We made observations from Aug. through Nov. in 1988 and 1989, and in April and May 1989. During each observation, we recorded activity in a 40 cm × 40 cm quadrat in an area where water column fish were foraging. This quadrat size ensured that fish inside the quadrat were no more than 5–7 body lengths apart, which is the upper range of literature values for distances between interacting fish (Seghers, 1981; Helfman, 1984; Grant, 1990). This quadrat size was too small, however, to contain the large groups that formed in some habitats. Therefore, we placed quadrats so as to encompass relatively discrete foraging locations, i.e., areas in which individuals moved in and out, but where fish usually did not feed in the immediate surrounding area.

We observed foraging activity by snorkeling, holding position about one meter downstream or to the side of the quadrat. Fish did not appear to be disturbed by a stationary observer. We used a tape recorder with a microphone attached to a snorkel to record numbers and species of fishes present and fish movements in and out of the quadrat for periods of 25–40 min. During most observations, we also recorded displacements or chases among foragers. A displacement involved one fish swimming laterally toward a target individual, which either shifted position or moved laterally back toward the aggressor. Chases involved an aggressor either swimming directly toward another fish, or approaching and pursuing a fish from behind. Finally, during some observations, we counted feeding strikes by dace. We counted all feeding

strikes made by the foraging group if the group was small and feeding activity was relatively low. Otherwise, we haphazardly selected focal individuals from the group for 1–2 min observations, attempting to watch as many different individuals during sessions as possible.

We transcribed taperecorded data by tabulating activity (i.e., initial group size, arrivals, departures, aggressive acts, feeding strikes) occurring in the quadrat during successive 5-sec intervals. We then calculated arrival, departure, and feeding rates of dace in a given quadrat (i.e., during a single 25–40 min observation) for 5-sec intervals when (1) only dace were present (“dace groups”), and (2) when another species was present (“heterospecific groups”). To test for effects of heterospecifics on dace behavior, we compared dace arrival, departure, and feeding rates between dace groups versus heterospecific groups having the same number of dace as the dace groups. When data for several group sizes (where group size was defined as the number of dace present at the beginning of a 5-sec interval) were available for both dace groups and heterospecific groups, we averaged rates across group sizes. To avoid biasing data by including poorly estimated rates, we only used estimates for a given group size if there were a sufficient number of 5-sec intervals so that the standard errors of estimated arrival and departure rates were <30% of the mean rates.

Pairs of rate estimates (for dace groups versus heterospecific groups) from observations on different dates or in different sites were used in Wilcoxon signed-ranks tests to evaluate the effects of other species on dace activity. These tests were one tailed (because our a priori hypothesis was that heterospecifics lowered the value of foraging sites for dace) and tested the following null hypotheses: (1) Dace arrival rates were not lower in groups containing other species; (2) Dace departure rates were not higher when other species were present; (3) Dace feeding rates were not lower when other species were present.

Results.—We compared dace arrivals and departures in single-species groups versus groups with a rainbow trout for nine observation sets; we also recorded feeding rate data for six of these sets. Trout ranged from approximately 6–15 cm total length, whereas dace averaged 5–7 cm total length. Arrival rates of dace were not significantly lower when a trout was in the quadrat (Table 1). Dace departure rates, how-

TABLE 1. EFFECTS OF RAINBOW TROUT ON DACE ARRIVAL AND DEPARTURE RATES (number $\cdot 5 \text{ sec}^{-1}$). Rates are means for groups containing the specified number of dace, either in a group of dace only or with a trout present. The number of 5 sec intervals used for each estimate is shown in parentheses.

Date†	Number of dace present	Arrival rate		Departure rate		
		Dace only	Trout present	Number of dace present	Dace only	Trout present
16 Aug. 88	3-4	0.74 (290)	1.21 (28)	3-5	0.72 (381)	1.33 (36)
17 Aug. 88	3	0.03 (35)	0.08 (274)	3	0.03 (35)	0.09 (274)
8 Sep. 88	0-1	0.03 (235)	0.04 (356)	1	0.02 (142)	0.13 (94)
9 Nov. 88	2-3	1.00 (63)	1.00 (29)	3-5	0.53 (171)	1.13 (38)
11 Nov. 89	1-2	0.48 (183)	0.18 (113)	2	0.13 (151)	0.36 (52)
11 Nov. 89	2-3	0.52 (71)	0.49 (55)	4	0.29 (41)	0.27 (74)
11 Aug. 89	4	0.18 (99)	0.22 (50)	4-5	0.16 (200)	0.06 (101)
5 Sep. 89	1	0.08 (306)	0.04 (92)	1	0.01 (306)	0.03 (92)
19 Sep. 89	0-1	0.41 (377)	0.37 (216)	1-2	0.16 (554)	0.49 (188)
Wilcoxon signed ranks test (1 tailed)		Ts = 22, P > 0.10			Ts = 6, P < 0.05	

† Observations from the same date were made at different sites.

ever, were higher in the presence of a trout in seven of nine observations, and the overall comparison was significant (Table 1). Average feeding rates for dace were significantly lower when a trout was present (Table 2), but trout rarely directly interfered with dace. Trout were aggressive toward dace only during two observations, and interspecific aggression rates were relatively low, averaging 0.017 and 0.016 incidents $\cdot 5 \text{ sec}^{-1} \cdot \text{dace}^{-1}$. Thus, the probability of a dace being chased by a trout was about 0.2 per minute. This rate was about 3.5 times lower than the average rate during observations when a dominant dace was the aggressor (Freeman, 1990).

In contrast to the effects of trout on departure rates, other cyprinids did not significantly affect arrivals or departures of dace (data for six observation sets, Table 3). Individuals of these species were of similar size to dace, approximately 5-8 cm total length. Note that, although we specifically tested for competitive effects, results of two-tailed tests would also be nonsignificant; i.e., dace were neither more nor less likely to forage at a site when other cyprinids were present. We quantified aggression among cyprinids during these observations and 17 other observations sets for which sample sizes were insufficient to estimate effects on dace arrivals and departures. Warpaint shiners displayed very low rates of aggression (0.006-0.011 incidents $\cdot 15 \text{ sec}^{-1} \cdot \text{dace}^{-1}$) toward dace during three observations; we observed no aggression between dace and warpaint shiners in six other observations, or between dace and creek chubs

(*Semotilus atromaculatus*), and only two displacements (in one out of 13 observations) with Tennessee shiners (*Notropis leuciodus*). We only have comparative feeding data for one observation set each with warpaint shiners or creek chubs present. When a warpaint shiner was present on 5 Oct. 1988, dace feeding rates declined from 0.121 to 0.037 strikes $\cdot 5 \text{ sec}^{-1} \cdot \text{dace}^{-1}$ (in groups of 1-3 dace). Conversely, dace feeding rates were unrelated to the number of creek chubs (0-4) present in the quadrat on 18 Sept. 1989 (weighted linear regression, $F = 0.66$, $P = 0.48$, $n = 5$; we could not estimate heterospecific effects on arrivals and departures because chubs were present in the quadrat for 97% of the observation time on that date).

TABLE 2. EFFECTS OF TROUT ON DACE FORAGING RATES. Values are means for groups with the specified number of dace, either in a group of dace only or with a trout present. The number of 5 sec intervals used for each estimate is shown in parentheses.

Date†	Number of dace present	Feeding strikes $\cdot 5 \text{ sec}^{-1} \cdot \text{dace}^{-1}$	
		Dace only	Trout present
8 Sep. 89	1-2	0.111 (155)	0.037 (110)
11 Nov. 89	1-2	0.176 (91)	0.125 (79)
11 Nov. 89	4	0.067 (30)	0.033 (61)
11 Aug. 89	3-5	0.150 (354)	0.100 (174)
5 Sep. 89	1	0.211 (298)	0.220 (91)
19 Sep. 89	1-2	0.114 (542)	0.092 (152)
Wilcoxon signed ranks test (1 tailed)		Ts = 1, P < 0.05	

† Observations from the same date were made at different sites.

TABLE 3. EFFECTS OF WATER COLUMN CYPRINIDS ON DACE ARRIVAL AND DEPARTURE RATES (number \cdot 5 sec⁻¹). Rates are means for groups containing the specified number of dace, either in a group of dace only or with a heterospecific present. The number of 5 sec intervals used for each estimate is shown in parentheses.

Date	Number of dace present	Arrival rate		Number of dace present	Departure rate	
		Dace only	Heterospecific present		Dace only	Heterospecific present
Groups with vs without warpaint shiners						
5 Oct. 88	1-3	0.52 (148)	0.37 (296)	2-4	0.74 (132)	0.83 (143)
Groups with vs without creek chubs						
27 Sep. 88	4	0.90 (187)	0.79 (14)	4-5	1.00 (321)	1.15 (27)
Groups with vs without Tennessee shiners						
23 Oct. 88	4	0.21 (19)	0.19 (27)	4	0.42 (19)	0.11 (27)
14 Apr. 89	1-2	0.60 (78)	0.58 (106)	1-3	0.81 (89)	0.80 (130)
16 Apr. 89	0	0.44 (70)	0.61 (23)	1-2	0.59 (112)	0.70 (39)
2 May 89	0-2	0.87 (128)	0.75 (104)	1-3	1.31 (102)	1.08 (88)
Wilcoxon signed ranks test (1 tailed)		Ts = 6, P > 0.1			Ts = 9, P > 0.1	

Discussion.—Grossman and Freeman (1987) showed that water column fishes at Coweeta overlapped extensively in microhabitat use and suggested that species generally did not compete for suitable microhabitat. Our results support this conclusion, in part, because dace entered and left foraging locations independently of the presence of other cyprinids. In addition, aggression between dace and heterospecifics was rare, whereas individual dace sometimes were more intensely aggressive toward conspecifics (Grossman and Freeman, 1987; Freeman, 1990). However, dace remained in foraging sites for less time and had lower feeding rates in the presence of rainbow trout. This suggests that rainbow trout lowered the value of a foraging site for dace, possibly by lowering food availability. Trout usually were not large enough to pose a predation threat to dace. Whether or not exploitative competition with trout lowered overall foraging success for dace would depend on the availability and value of alternative sites. Hill (1989) provided evidence that interspecific competition did not affect microhabitat use by rainbow trout and dace at Coweeta, because both species foraged at velocities close to their energetic optima. Similarly, Grossman and Boulé (1991) experimentally demonstrated that dace do not affect microhabitat use by trout. Our results, together with Hill's study, suggest that rainbow trout may have altered the spatial distribution of foraging dace without affecting dace microhabitat use.

Our data set was limited by the low frequency

with which other, less abundant species foraged with dace. Our conclusions are therefore tentative, especially with respect to the effects of other cyprinids on dace behavior. The lack of significant interactions with other cyprinids, however, is consistent with the low frequency of intraspecific competition or social attraction among dace (Freeman, 1990). Interestingly, dace displayed a response to an introduced species, rainbow trout. Data on foraging interactions between dace and brook trout (*Salvelinus fontinalis*), the native salmonid in this system, could help clarify the extent to which dace interactions with rainbow trout reflect the absence of resource partitioning mechanisms between species that did not coevolve.

The approach of examining group dynamics in relation to species composition may provide a direct method of testing for interspecific interactions, mutualism as well as competition, among fishes that forage in groups. The advantage of this approach is that one can evaluate the significance to foragers of species segregation or association. For example, species differences in vertical distribution within groups may reflect differences in evolutionary adaptation to habitat factors rather than interactive segregation (Mendelson, 1975; Grossman et al., 1987; Gorman, 1988b). Furthermore, interspecific differences in mean water column position may or may not result in trophic partitioning, and it may be difficult to quantify the effects of vertical segregation on foraging success in natural foraging groups. If, however, segregation does

reduce competition for limited food resources, then individuals may be more likely to join (or less likely to leave) a heterospecific group than an equivalently sized group of conspecifics. Similarly, where mutualistic interactions among foragers are suspected, analyzing group dynamics may allow one to quantify the strength of attraction among conspecifics or heterospecifics in field situations where actual benefits to individuals are difficult to measure.

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