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Intraspecific interactions influence size specific depth distribution in *Cottus bairdi*

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Synopsis

We tested depth selection by different sizes of mottled sculpin, *Cottus bairdi*, in a southern Appalachian stream. Field observations indicated that, during one hour periods, both small (<50 mm SL) and large (≥55 mm SL) individuals move within an area less than 0.50 m². Individuals of both sizes, placed in field enclosures, preferred deep microhabitat. When large fish were placed in cages with small fish, small fish initially spent more time in slope and shallow microhabitats. Average interfish distances were not correlated with their absolute size differences, suggesting *C. bairdi* interactions may involve both predation and competition. In streams, size-related differences in microhabitat depth may result more from intraspecific interactions than from size-specific depth preferences.

Introduction

In this study we experimentally tested depth selection by *Cottus bairdi*, the mottled sculpin, in a southern Appalachian stream. Previous observational work at this site showed that small (<40 mm SL) sculpins generally occupied shallower microhabitats than larger conspecifics (Grossman & Freeman 1987). We did not know, however, if smaller *C. bairdi* actually preferred shallower habitats or if they were excluded from deeper areas by larger sculpins. Predation or competition may contribute to differential depth selection. This distinction would be important for predicting the suitability of a particular habitat for recruitment and/or survival of juvenile *C. bairdi*. Thus, using in-stream enclosures, we addressed two questions: (1) do large and small sculpins both prefer deep microhabitats?, and (2) do small individuals shift to shallower habitats in the presence of large sculpins?

Materials and methods

Our study consisted of two parts: (1) field observations to determine the validity of conducting *C. bairdi* behavior experiments in 1 m² enclosures, and (2) enclosure experiments to investigate effects of large *C. bairdi* on depth preference by smaller and similarly-sized conspecifics. We conducted all observations and experiments from July 1986 through September 1987 at the U.S. Forest Service Coweeta Hydrologic Laboratory, in the southern Appalachian Mountains (Macon Co., North Carolina, U.S.A.).

In the first part of our study, we recorded movements by unenclosed *C. bairdi* during 1 h periods between 1100 h and 1700 h on 6 d during July and September 1987. We observed *C. bairdi* by snorkeling upstream until we located an undisturbed individual. Upon sighting a fish, we recorded its standard length (mm SL) and noted its location.

We also recorded distance, direction and frequency of its movements. From these data we estimated: (1) total area encompassing all movements, (2) total distance travelled (summed over all movements), and (3) total activity time. We defined activity time as the number of minutes during which the fish moved at least once every three minutes. If unenclosed *C. bairdi* stayed within 1 m², then we could justify using enclosures of that size. Documenting distance travelled and time spent active would allow us to compare fish behavior in the field and in enclosures.

The second part of the study involved using movable enclosures. We constructed two enclosures with polyvinylchloride (PVC) pipe frames and hardware cloth (0.64 cm mesh) sides and bottom. Enclosures measured 1 m², and were 0.5 m tall. The bottom formed a depth gradient in which deep, slope, and shallow habitats each composed one-third of the area. Shallow habitat was 12 cm higher than the deep, and the slope gradient was approximately 20°. We covered the bottom with plastic sheeting and epoxied uniformly-sized gravel (5–10 mm diameter) to the plastic in order to evenly cover the bottom. On nights prior to experiments, we oriented enclosures in the stream with the depth gradient perpendicular to water flow (each habitat received inflowing water), allowing relatively uniform current velocity across each habitat. Water depths in enclosures depended on stream water level during experiments, but ranged from 4 to 10 cm in shallow and 12 to 23 cm in deep habitats. After enclosures were in place, we poured loose gravel on top of epoxied gravel to provide fish with a relatively natural substrate.

The first two trials were each conducted over 2 d; we completed all subsequent trials in 1 d each in order to minimize effects of hunger on *C. bairdi* behavior. One-day trials began in the morning by collecting, with an electrofisher, small (<50 mm SL) and large (>55 mm SL) *C. bairdi*. We placed a small individual in one enclosure (chosen by a coin toss) and both a small and a large conspecific in the other enclosure. Fish were released mid-slope in the center of the enclosures and allowed to acclimate for 2 h. After acclimation, we recorded fish locations and movements for 1 h. We

then added a large *C. bairdi* to the enclosure started with a small fish alone and removed the large individual from the other enclosure. We again recorded fish locations and movements after a second 2 h acclimation period. Finally, we reversed treatments, by removing or replacing large *C. bairdi*, allowed fish to reacclimate 2 h, and repeated observations. By simultaneously conducting two trials with opposite treatments at any time, this procedure controlled for time of day effects on *C. bairdi* movement and interactions. Methods for 2 d trials were similar except that large fish were removed or added (depending on starting conditions) in the evening of the first day. We also used 1 d procedures to test for effects of interference between *C. bairdi* of similar size (>50 mm SL) on depth preference.

If *C. bairdi* of all sizes prefer deeper water, then smaller individuals should only occupy shallower habitats when threatened by large conspecifics. In other words, small sculpins should shift to slope or shallow habitats in the presence of a large *C. bairdi*, and return to the deep upon removal of a large individual. These expectations include the following assumptions: (1) sculpin movements are not so restricted by 1 m² enclosures that individuals use areas they normally avoid; (2) large *C. bairdi* choose the deep side of enclosures; (3) a small fish in an enclosure perceives the presence or absence of a conspecific; and (4) small *C. bairdi* behavior is unaffected by previous experience in an enclosure (i.e., small *C. bairdi* depth preference should be consistent among observations in which a larger conspecific was either present or absent). Field observations provide a basis for evaluating assumption 1, whereas enclosure experiments allow tests of assumptions 2 and 4. We could not directly test assumption 3.

We tested for depth preference in enclosures by comparing time allocation among habitats to a uniform distribution (i.e., no preference; χ^2 test). Subsequently we tested for heterogeneity in depth preference within treatments using a χ^2 test. To evaluate effects of size difference on intraspecific interactions, we correlated minimum and average distances between individuals, during their first observation together, with the difference in their standard lengths.

Results

Enclosures apparently were large enough to encompass usual *C. bairdi* movements. During 60 min field observations, 12 unenclosed *C. bairdi* all moved in areas that were less than 1 m², and ranged from 0.05 m² to 0.50 m². Total distances travelled during observations were similar for unenclosed and enclosed fish (Table 1). Both enclosure and field observations indicated that small individuals may move more frequently than large *C. bairdi*, although unenclosed fish generally were more active than those used in experiments (Table 1). Hence, although fish behaved differently in enclosures, the enclosures did not appear to restrict the range of individual movement.

Large *C. bairdi* generally chose deep habitat in enclosures, thus supporting the second assumption of our experimental design. Seven of 8 large individuals used in trials with small *C. bairdi* strongly preferred deep habitat (χ^2 tests, $p < 0.001$), remaining in the deep for at least 70% of any 60 min observation (Table 2). The other large sculpin remained on the deeper part of slope habitat during one observation. Averaged across all 8 trials, large *C. bairdi* spent 89% of observation time in the deep, and 4 individuals spent 100% of observation time in the deep.

Small *C. bairdi* generally did not prefer shallower habitats than large fish; when in an enclosure alone, 6 of 8 small individuals preferred deep habitat (Table 2). Averaged across all 8 trials, small *C. bairdi* alone in enclosures spent 77% of observation time in the deep.

We could not directly test the third assumption, that small *C. bairdi* were aware of the presence of a large fish in an enclosure. Mean minimum distance between fish was 50 cm (S.D. = 29 cm), which suggested that *C. bairdi* frequently did see each other. A more difficult problem was whether small *C. bairdi* always could detect removal of a large individual, especially in trials in which large fish were mostly inactive. If small individuals failed to detect removal of large *C. bairdi*, then small individuals might have behaved as though the large fish were still present during subsequent observations. In fact, small *C. bairdi* depth preferences tended to differ between subsequent observations under the same treatment (i.e., large *C. bairdi* present or absent), thus violating our fourth assumption. This within-treatment heterogeneity was significant in 6 trials (Table 2) and suggested that experience in enclosures may have affected small *C. bairdi* behavior. Therefore, we could not pool observations within treatments to evaluate effects of large individuals on small *C. bairdi* depth preference. We could, however, use the first observation of each experiment to compare depth selection between small *C. bairdi* that were alone versus with a large *C. bairdi*. Small *C. bairdi* behavior in initial observations could not have been differentially affected by previous experience in enclosures, because we made these observations in the morning, approximately 2 h after either only a small individual or both a small and a large *C. bairdi* had been placed in an enclosure.

Depth selection by small individuals apparently was influenced by large *C. bairdi* presence. During

Table 1. *C. bairdi* activity during 1 h periods, expressed as distance travelled and time active. Values shown are means, with ranges in parentheses; sample sizes are 4 small and 7 large *C. bairdi* for field observations, and 8 small and 16 large individuals in enclosures.

Fish size, standard length ($\bar{x} \pm 1$ s.d., mm)	Total distance moved (cm)		Time active (min)	
	Field	Enclosures	Field	Enclosures
Small, 42 \pm 4	159 (53-331)	193 (24-385)	30 (10-49)	18 (1-41)
Large, 64 \pm 10	184 (0-473)	96 (0-423)	16 (0-47)	4 (0-17)

initial (morning) observations, small individuals always spent 100% of observation time in the deep while alone, in contrast to 39, 47, 80, and 80% when with large *C. bairdi* (Table 2). The probability of obtaining this difference between treatments by chance was 0.05 (Mann-Whitney U test, $U = 16$). In addition, in all 4 trials in which small *C. bairdi* were initially alone, these individuals shifted to spend some time in slope and/or shallow habitats when we added a large *C. bairdi* (Table 2). These results suggested that, in enclosures, small *C. bairdi* preferred deeper habitats, and initially were more likely to move into shallower habitats in the presence of a larger conspecific.

Experiments with fish of similar size failed to demonstrate intraspecific effects on depth selection. Only 1 of 4 trials provided any evidence that large *C. bairdi* retreated to shallower habitat in the presence of another large conspecific (Table 3).

Results were complicated by the behavior of 1 large individual that remained in shallow habitat during all observations, and by significant within-treatment heterogeneity in 2 other trials (Table 3). Comparing initial observations (as in trials with small and large individuals), there was no difference between time spent in the deep by large *C. bairdi* alone versus with another fish.

In addition, there was no significant correlation between mean distance separating *C. bairdi* and the difference in their standard lengths ($r = -0.35$, using distances between individuals during their first observation together). Similarly, minimum distance between individuals during their first observation together was not significantly correlated with their size difference ($r = -0.15$). Although 7 pairs averaged over 75 cm between fish, pairs with the smallest average separating distances differed in length by only 14 mm (mean distance =

Table 2. Small (<50 mm SL) *C. bairdi* depth selection during 1 h periods with a large fish either present or absent (N.P.). Values represent percentages of time that each fish spent in deep/slope/shallow microhabitats. Different superscripts indicate significance within treatment differences in time allocation by small fish (χ^2 tests, $p < 0.01$).

Trial date	Fish size, SL (mm)	Approximate observation time (h)			
		1000–1100 h	1300–1400 h	1600–1700 h	
23 July	Small, 42	100/0/0 ^a	87/7/7	100/0/0 ^a	
	Large, 68	N.P.	100/0/0	N.P.	
2 August	Small, 41	100/0/0 ^a	25/23/52	100/0/0 ^a	
	Large, 71	N.P.	100/0/0	N.P.	
20 April	Small, 44	100/0/0 ^a	57/7/37	58/0/42 ^b	
	Large, 56	N.P.	100/0/0	N.P.	
23 July	Small, 37	80/20/0 ^a	67/33/0	37/63/0 ^b	
	Large, 68	100/0/0	N.P.	100/0/0	
2 August	Small, 42	80/20/0 ^a	100/0/0	100/0/0 ^b	
	Large, 77	70/1/29	N.P.	0/100/0	
20 April	Small, 48	47/28/25 ^a	0/42/58	0/0/100 ^b	
	Large, 58	70/30/0	N.P.	100/0/0	
Two day trials		Day one		Day two	
		1000–1100 h	1300–1400 h	1000–1100 h	1300–1400 h
17–18 July	Small, 40	100/0/0 ^a	100/0/0 ^a	80/20/0 ^b	0/100/0 ^c
	Large, 79	N.P.	N.P.	98/2/0	90/7/3
10–11 July	Small, 35	39/0/61 ^a	18/0/82 ^b	90/5/5 ^c	55/27/18 ^d
	Large, 88	87/0/13	100/0/0	N.P.	N.P.

26 cm) and by as much as 53 mm (mean distance = 43 cm).

Our results suggest the following: (1) unenclosed sculpins normally move within an area less than 1 m² during an hour; (2) both large and small fish prefer deeper habitats; and (3) large individuals may displace smaller *C. bairdi* from preferred habitats.

Discussion

Enclosure experiments demonstrated that all sizes of *C. bairdi* generally preferred deeper habitats when presented with a depth gradient. Small individuals (<50 mm SL), however, tended to use shallower habitats in the presence of a large conspecific. Hence, field observations of microhabitat depth differences among *C. bairdi* size-classes (Grossman & Freeman 1987) may have resulted more from intraspecific interactions than from size-specific depth preferences. The extent to which small *C. bairdi* shifted to shallow habitats varied among enclosure trials suggesting that intensity of intraspecific effects varies with experience (e.g., outcome of previous interactions) and condition (e.g., hunger level, reproductive condition) of individual fish.

Schlosser (1987) reported that juveniles of three stream fishes shifted from pools to shallower riffles or raceways in an artificial stream when piscivorous

centrarchids were added to pools. Similarly, small sculpins used shallow water as a refuge from a centrarchid predator in a laboratory test (Anderson 1983). In our experiments, small *C. bairdi* may have avoided larger individuals to evade attack; however, we observed only one incidence of a large *C. bairdi* directly approaching a small individual. Downhower & Brown (1979) reported that cannibalism in this species only was possible if the attacking *C. bairdi* was at least 40 mm larger (in total length) than its prey. We therefore expected, and failed, to find a positive relationship between size difference in pairs of individuals used in experiments and their average distance apart. Conversely, if competition influenced dispersion then we would also expect similarly-sized fish to avoid each other. Lack of correlation between size difference and avoidance thus suggested *C. bairdi* interactions vary and may involve both predation and competition.

Ontogenetic habitat shifts are common in freshwater fishes. For example, Brandt (1986) reported that juvenile slimy sculpins, *Cottus cognatus*, in Lake Ontario generally occupied shallower depths than large individuals. In the absence of experimental evidence, however, it may be unclear whether habitat differences reflect biotic interactions or size-specific habitat requirements. Our results suggest that small mottled sculpins do not prefer shallower depths than larger individuals, but shallow areas may provide alternative microhab-

Table 3. Depth selection trials with two large (similarly-sized) *C. bairdi*. Approximate 1 h observations, with a second fish either present or absent (N.P.). Values represent percentages of time that each fish spent in deep/slope/shallow microhabitats. Different superscripts indicate significant within treatment differences in time allocation (χ^2 tests, $p < 0.005$).

Trial date	Fish size, SL (mm)	Approximate observation time (h)		
		1000-1100 h	1300-1400 h	1600-1700 h
16 Sept.	Large, 60	0/0/100 ^a	0/0/100	0/0/100 ^a
	Large, 51	N.P.	100/0/0	N.P.
28 April	Large, 50	93/7/0 ^a	100/0/0	95/4/1 ^a
	Large, 64	N.P.	100/0/0	N.P.
16 Sept.	Large, 54	100/0/0 ^a	75/25/0	77/2/22 ^b
	Large, 62	100/0/0 ^a	N.P.	0/100/0 ^b
28 April	Large, 54	17/12/72 ^a	92/3/5	100/0/0 ^b
	Large, 64	100/0/0 ^a	N.P.	100/0/0 ^a

itats for small sculpins faced with intense intraspecific predation or competition. The abundance of potential refugia provided by cobbles in natural streams may reduce intraspecific effects on habitat use; limited results with cobbles added to enclosures indicate that small sculpins sometimes remain in deep habitat under a cobble in the presence of a large fish (Deanna J. Stouder & Mary C. Freeman, personal observation). In conclusion, use of shallower microhabitats by small sculpins may depend on local population size structure and refuge availability, but probably does not reflect preference for shallow areas.

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