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Parallel swims as a means of intra- and interspecific assessment in stream fishes

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Synopsis

Several North American minnow species are known to engage in the action pattern 'parallel swimming', an activity that allows males competing for nests or nesting sites an opportunity to assess each other. These agonistic displays have been hypothesized to occur only between males of similar size. We provide evidence to support this hypothesis for two minnow species and a sucker species. Competition is strong both intra- and interspecifically for nest sites and we document the occurrence of interspecific parallel swims between three species.

Animal contests are often settled by ritualized displays that allow participants to assess each other's fighting ability and settle disputes nonviolently, thereby avoiding potentially costly fights that they are unlikely to win (Parker 1974, Enquist et al. 1990). In many cases, opponents are expected to escalate to fighting only if they are of similar ability. For example, competing red deer stags assess competitors in a series of displays that escalate if the challenger is able to match or beat a defender. Stags of similar fighting ability will engage in a parallel walk, enabling the males to carefully assess each other. Contests usually end at this stage, but if males still appear to be evenly matched, fighting ensues (Clutton-Brock & Albon 1979).

Contests between male stream fishes for breeding sites or females is common. This is especially true for species of nest-building fishes, which compete for limited nesting sites or existing nests. Although aggression between males of such species is intense, fighting is rare (Reighard 1910, Miller 1964). Contests between males involve chases, frontal displays, and parallel swims that are similar to the parallel walks of red deer (Reighard 1910, Miller 1964, Ross 1977). Parallel swims occur when resident and challenger males swim side by side for some distance from the nest, and are longer in distance and duration than the lateral displays of many fishes (e.g. cichlids). These complex displays were first described by Reighard (1910) for creek chubs *Semotilus atromaculatus* and have also been observed in other North American minnows, including species of *Cyprinella* (Outten 1958, Stout 1975, Rabito & Heins 1985), *Exoglossum* (Maurakis et al. 1991), *Luxilus* (Raney 1940, Outten 1957, Miller 1964, Vives 1990), *Lythrurus* (Hunter & Hasler 1965), *Nocomis* (Vives 1990), *Notropis* (Miller 1964), *Pteronotropis* (Johnston personal observation), and hybrid *Notropis rubellus* × *Luxilus cornutus* (Miller 1964). Similar parallel displays have

been observed in *Campostoma* (Miller 1962) and *Pimephales* (Vives 1988, Johnston personal observation), but are not as long in duration and distance travelled. Parallel swims have also been reported for suckers (Page & Johnston 1990), salmon (Keenleyside & Yamamoto 1962), and darters (Grant & Colgan 1984). Although many of the above authors note that parallel swim displays occur between males of similar size, no data have been presented to support this observation. If parallel swims are a mechanism for assessment between males to avoid fights they should only occur between males of similar size. We quantified the size of displaying males to assess the validity of this hypothesis.

While conducting this study, we observed that parallel swims do not occur only intraspecifically, but also between similar sized males of different species. Use of identical spawning habitat and synchronous breeding seasons creates conditions where males of many stream fishes must compete both intra- and interspecifically for nests and nest sites. Because these fishes use similar displays for intraspecific encounters, they would be predicted to use these same displays for encounters with other species. Interspecific parallel swims were first noted by Vives (1988) for *Nocomis biguttatus* and *Luxilus cornutus*. In this paper we expand the number of species known to engage in interspecific parallel swims and present the frequency of such encounters compared with that of the total number of parallel swims.

Methods

Study site and species

This study was conducted in two small drainage ditches in Champaign County, Illinois. The water in both is clear, and the substrate is gravel, sand and silt. Both streams consist primarily of run (glide) habitat with few pools or riffles. Our observations for the two sites are combined.

These small tributaries are used for spawning by creek chubs *Semotilus atromaculatus*, central stonerollers *Campostoma anomalum*, striped shiners *Luxilus chrysocephalus* and creek chubsuckers *Erimyzon oblongus*. Although there is temporal variability in the spawning periods of these species, they overlap throughout most of the spawning season. All four species compete both intra- and interspecifically for spawning nests, built primarily by male creek chubs.

To test our prediction that parallel swims occur primarily between similarly sized males, we made focal observations on males of three species known to use this display during contests: striped shiners, creek chubs and creek chubsuckers. Although central stonerollers are known to use a display similar to the parallel swim during aggressive encounters (Miller 1962), we did not observe it.

Observations

Observations of fishes were made from stream banks with the aid of polarized sunglasses. Most (95%) of the data were taken by one observer. Fishes were actively competing for nest sites during observation periods. Data were taken for creek chubs (n = 17 individuals) from mid-March to mid-May of 1990 and 1992. Focal observations of nest-building (or resident) males were made for 15–30 minutes, and all aggressive encounters and the relative size of the challenging male were noted. Male size was visually estimated relative to the resident male as same size (no discernable difference in size), smaller (obviously smaller, by approximately 3 cm or more), or larger (obviously larger, by approximately 3 cm or more). Five minute focal samples were similarly made for striped shiner males (n = 15) on 11 June 1990 and creek chubsucker males (n = 10) on 8 May 1990. Counts of parallel swim data include only encounters with different individuals; multiple parallel swims with the same individual were only counted once. The range of male size (SL, standard length) for *E. oblongus* was 95–150 mm SL (mean = 124.6 mm, SD = 16.4, n = 21); the range of male size for *S. atromaculatus* was 115–185 mm SL (mean = 145.8 mm, SD = 18.4, n = 36). Fishes were captured and measured following observations and on separate collecting trips. Data on length of male *L. chrysocephalus* were not taken.

Table 1. Aggressive behaviors observed for opponent males of three size categories of three species. Opponent size categories are relative to the size of the resident male.

Species	Behavior	Number of events per opponent size category			X^2	p
		Smaller	Same size	Larger		
Semotilus atromaculatus	Parallel swim	3	30	4	30.7	< 0.005
	Frontal display	61	6	10	73.4	< 0.005
	Chase	250	21	20	36.2	< 0.005
Erimyzon oblongus	Parallel swim	3	17	0	24.7	< 0.005
	Frontal display	2	9	1	9.5	< 0.05
	Chase	129	20	0	194.3	< 0.005
Luxilus chrysocephalus	Parallel swim	1	25	3	36.7	< 0.005
	Frontal display	41	15	8	35.4	< 0.005
	Chase	193	11	21	279.1	< 0.005

Results

The number of parallel swims, chases and frontal displays for opponent males in three size categories for three species is shown in Table 1. Within each species, more parallel swims occurred between males of similar size than between males of different size (smaller or larger). Chases were more common than parallel swims and frontal displays, and were directed most often at smaller opponents in all three species. Frontal displays were also used most commonly on small opponents in *S. atromaculatus* and *L. chrysocephalus,* but were most common between similarly-sized *E. oblongus.*

Twelve interspecific parallel swims were observed in this study. One was between male *E. oblongus* and *S. atromaculatus,* six were between male *E. oblongus* and *L. chrysocephalus,* and five were between male *S. atromaculatus* and *L. chrysocephalus.* All of these displays were between males of similar size. Interspecific parallel swims accounted for 11% of the total parallel swims observed.

Discussion

Our data suggest that parallel swims occur most frequently between males of similar size in the three species examined, supporting our contention that the display is a form of assessment. These results agree with the observations of other authors, including Miller (1962, 1964) for *Campostoma anomalum, Semotilus atromaculatus, Luxilus cornutus,* and *Notropis rubellus;* Vives (1990) for *Nocomis biguttatus*; Ross (1977) and Reighard (1910) for *S. atromaculatus*; and Maurakis et al. (1991) for *Exoglossum* spp. Interestingly, observations indicate that similarly-sized male *Exoglossum* also use coloration (light or dark) as a means of assessment, as parallel swims between darker males lasted longer than those between lighter-colored males (Maurakis et al. 1991).

Interspecific parallel swims accounted for 11% of parallel swims observed in our study and included all combinations of the three study species. Because all of these species use the parallel swim display for intraspecific assessment, and all are competing for nest positions or sites simultaneously, it is not suprising that they also use the display during encounters with males of other species.

The use of common nest sites by several species with complex social systems provides an ideal system for the study of animal contests. Not only are complex intraspecific displays used, but these same displays are recognized by several species. We know of no other system which provides such an opportunity for study, and it is hoped that these fishes will be used for future experimental and observational studies.

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