Agonistic Behavior, Social Dominance, and Food Consumption of Brook Trout and Rainbow Trout in a Laboratory Stream

Louis A. Helfrich, *Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061*

John R. Wolfe, Jr., *Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061*

Peter T. Bromley, *Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061*

Abstract: Agonistic behavior and social dominance relationships between similar-sized, wild, adult brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) were examined in a laboratory stream. Frequency of movements, aggressive encounters, and consumption of food items by trout when held as single specimens, intraspecific pairs, and interspecific pairs were compared. Rainbow trout were more mobile, aggressive, and successful foragers on drifting prey than brook trout; however, neither species appeared to possess a competitive advantage in establishing social dominance or displacing interspecific rivals. Brook trout were dominant in 9 of 14 interspecific matches. Female trout were dominant in 6 of 10 opposite-sex matches. Dominant trout, regardless of species or sex, exhibited significantly greater mobility, aggressiveness, and feeding success than subordinate trout.

Stream surveys conducted in the southeastern United States during the last century have documented a significant reduction in the distribution of native brook trout and a concurrent expansion of rainbow trout into waters originally inhabited by brook trout (Lennon 1967, Jones 1978, Kelley et al. 1980). The marked compression in the range of brook trout in southern

Appalachian mountain streams has been attributed to several factors including water quality degradation, habitat destruction, and over-exploitation by anglers. In addition, continuous upstream encroachment by rainbow trout suggests that interspecific competition has played a major role in the observed displacement of brook trout.

Brook trout and rainbow trout have evolved allopatrically in the eastern and western portions of North America, respectively (MacCrimmon and Campbell 1969, MacCrimmon 1971). Rainbow trout were introduced into Virginia and North Carolina beginning in 1880 (MacCrimmon 1971) and the 2 species are now sympatric in many streams in the southeastern United States. Their ecological and behavioral similarities indicate that intense competition could occur between sympatric populations (Newman 1956).

A number of authors have investigated agonistic behavior in rainbow trout (Stringer and Hoar 1955; Hartman 1965; Jenkins 1969, 1971; Slaney and Northcote 1974) and brook trout (Moyle 1969, Griffith 1972, McNicol and Noakes 1981, Noakes 1980). However, only Newman (1956) has examined direct behavioral interactions between rainbow and brook trout. He concluded that brook trout dominated even slightly larger rainbow trout in small tanks, but rainbow trout appeared "aggressively adequate" in larger tanks.

His study, which was based largely on interactions of juvenile, hatchery-reared trout in standing water aquaria, may not be representative of social encounters between wild, adult brook and rainbow trout in streams. Hatchery fish express different behavioral patterns (Moyle 1969) and levels of aggression (Fenderson et al., 1968) than wild fish, and social behavior is frequently altered by water velocity (Kalleberg 1958, Keenleyside 1962, Reimers 1968).

In this study we contrast the abilities of similar-sized, wild, adult brook and rainbow trout to achieve social dominance and forage successfully in a flowing water environment. If rainbow trout are displacing brook trout in Appalachian streams, we hypothesize that they are superior competitors for social dominance (rank) and available food and space resources.

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Methods

The present study examines relative agonistic behavior, social dominance relationships, and food consumption patterns of brook and rainbow trout when confined as single specimens, intraspecific pairs, and interspecific pairs in a laboratory stream. Agonistic behavior includes aggressive (fight)

and submissive (flight) responses (Scott and Fredericson 1956) and is one of the most explicit mechanisms used by coexisting vertebrates to acquire limiting resources (Chapman 1962, Wilson 1975).

Fish were observed in one section (1.1 × 1.1 × 0.5 m deep) of an oval-shaped fiberglass tank (16 × 1.1 × 0.5 m deep). An opaque, aqua-colored outer tank wall minimized outside disturbance and a clear Plexiglas inner wall permitted an unobstructed view of the fish. The observer was concealed in a black polyethylene blind located in the center of the tank.

Incandescent and fluorescent bulbs suspended above the tank provided an average light intensity of 387 lux at the water surface during the light cycle. Photoperiod was maintained on a 14-hour light, 10-hour dark cycle. Water current velocity was maintained at 8.7 cm/s and water depth was 25 cm. Temperature was maintained at 14 ± 1 C by recirculating water through a refrigeration unit. Dissolved oxygen, pH, and total alkalinity averaged 10 mg/l, 6.6, and 40 mg/l, respectively.

Adult brook and rainbow trout were collected by electrofishing during July, 1977 from self-sustaining populations in the headwaters of Little Stony Creek, Giles County, Virginia and Peach Orchard Creek, Buncombe County, North Carolina. Since these streams have not been stocked in the last 15 years, all experimental fish were considered representative of wild stocks. From these collections, a total of 20 brook and rainbow trout of similar size and age were selected for observation. Brook trout averaged 169 (±20.3) mm fork length and 43.8 (±15.5) g live weight; rainbow trout averaged 167.6 (±18.0) mm FL and 43.2 (±12.8) g live weight. Larger body size is widely regarded as the principal determinant of social status (Newman 1956, Chapman 1962, Reimers 1968, Symons 1968). Therefore, in this study only similar-sized fish were used to reduce the influence of body size. Mean differences in body length and weight for all paired matches were 9.0 (±7.3) mm FL and 5.2 (±3.7) g, respectively.

Trout were observed 3 hours per day for 14 days in 3 experimental situations: as single specimens, in intraspecific pairs, and in interspecific pairs. Observations were made during the first or last hour of available light, alternating on consecutive days, and at 2 other randomly selected hours each day. The frequency of movements (changes in position within a 3 dimensional grid system superimposed on the Plexiglas of the stream tank), feeding success (number of food items consumed), and nips (biting with physical contact) were recorded for each fish. Trout were fed once per day, alternating daily between the first and last hour of available light, a diet of invertebrates and earthworms at 2% trout body weight. Equal numbers of similar-sized food items were introduced as subsurface drift by flushing each food item from the blind through a plastic tube extending into the tank. Only consumed food items were recorded.

Qualitative behavioral observations on the following agonistic responses were made visually and recorded on videotape: approach (Symons 1968, Jenkins 1969), frontal display (Keenleyside and Yamamoto 1962, Hartman 1965, Fenderson et al. 1968), lateral display (Newman 1956, Kalleberg 1958), wig-wag display (Hartman 1965, Jenkins 1969, North 1979), submissive display (Newman 1956, Keenleyside and Yamamoto 1962), charge (Kalleberg 1958), chasing (Keenleyside and Yamamoto 1962), reciprocal circling (Newman 1956), parallel swimming (Kelleberg 1958), nip threat (Stringer and Hoar 1955), and flight (Jenkins 1969). All of these behavioral activities were readily discernible and consistent with published descriptions. Rank between fishes in intraspecific and interspecific matches was determined subjectively from a composite analysis of these responses and a consideration of supplanting (displacement). Supplanting occurs when one individual approaches another, with or without threat behavior, and the other individual leaves the area (Brown 1975). Supplanting was used as the principal indicator of social dominance between paired fishes in this study.

Statistical analyses were performed with non-parametric procedures (Holander and Wolfe 1973). Comparisons of activity, nips, and feeding success rates within pairs and between pairs were made with the Fisher Sign Test and the Wilcoxon Rank Sum Test, respectively. Comparisons of dominance between species and sex were made with the Binomial Test. Statistical significance was assumed at the 5% level ($P < 0.05$).

Results and Discussion

Single Specimens

When held as single specimens to establish reference patterns of activity and feeding success rates, individual rainbow trout were significantly more mobile than brook trout (Table 1). However, despite this almost 2-fold difference in mobility, food consumption by both species was similar. The greater mobility exhibited by rainbow trout cannot be attributed to increased foraging activity as a result of food deprivation since food consumption was nearly identical and <50% of the food items offered was consumed. The presence of food items stimulated movement among individuals of both species, but rainbow trout were consistently more active than brook trout even in the absence of food.

Intraspecific Pairs

When held as intraspecific pairs, rainbow trout were more mobile than brook trout, but these differences were not significant (Table 1). The presence of another fish appeared to inhibit movement since individuals of both

Table 1.   Mean Number of Movements, Food Items Consumed, and Nips Delivered Per Hour by Brook and Rainbow Trout Held As Single Specimens, Intraspecific Pairs, and Interspecific Pairs

Treatments	N	Observation Time (hours)	Movements	Food Items Consumed	Nips Delivered
Single Trout:					
Brook	5	60	5.6	0.43	
Rainbow	5	60	11.0[a]	0.46	
Intraspecific Pairs:					
Brook	6	58	4.7	0.47	0.40
Rainbow	6	58	5.8	0.47	6.78[a]
Interspecific Pairs:					
Brook	14	160	6.9	0.30	0.93
Rainbow	14	160	9.0	1.14[a]	1.78

[a] Significantly larger values ($P < 0.05$).

species in intraspecific matches were less mobile than those held singly. Mobility of rainbow trout was more depressed by the presence of a conspecific than was that of brook trout. Food consumption was not influenced by the presence of conspecifics and was similar to that of trout held as single specimens. Rainbow trout were significantly more aggressive, attacking (nipping) conspecifics nearly 3 times more frequently than did brook trout.

Interspecific Pairs

In interspecific matches, as in intraspecific matches, rainbow trout were more mobile and more aggressive than brook trout, but these differences were not significant (Table 1). Mean locomotor activity for both species was higher than that observed in intraspecific matches, suggesting that the presence of the opposite species increased mobility more than a conspecific. Rainbow trout attacked brook trout almost twice as frequently as brook trout attacked rainbows. The mean nip rate for rainbow trout was substantially lower in interspecific than intraspecific matches, whereas the mean nip rate for brook trout was higher in interspecific than intraspecific matches. Thus, while rainbow trout tended to attack conspecifics more frequently than brook trout, the opposite was true for brook trout.

Differences in mobility and aggression between rainbow trout and brook trout may reflect innate species-specific habits and behavioral responses. Rainbow trout tended to roam freely about the observation section, nipping whenever contestants were not in threat display. In contrast, brook trout restricted their movements and remained in preferred positions, generally toward the bottom of the laboratory stream, attacking only when closely approached by another fish. Newman (1956) suggested that the lower nipping

frequency, greater use of threat behavior, and more elaborate threat display in brook trout than rainbow trout may indicate a more advanced social behavior in which potentially injurious fighting is suppressed.

Another potential explanation for the observed disparity in mobility and aggression between these species is that our rainbow trout, as decendants of hatchery stocks, may have been particularly active and aggressive. Our rainbow trout were from self-sustaining "wild" populations that have been isolated from hatchery stocks for at least 15 years, but it is conceivable that continuous artificial selection at hatcheries could have contributed to the expression of aggression and mobility observed. Fenderson et al. (1968) found that hatchery-reared Atlantic salmon parr (*Salmo salar*) exhibited a higher intensity of aggressiveness than wild stocks and speculated that the conditioning effect of crowding, mass feeding, and other continual disturbances at hatcheries elevates excitation levels that may in time select for overly aggressive individuals. Moyle (1969) reported higher levels of aggression in "domestic" hatchery-reared brook trout fry than F-1 "wild" brook trout fry reared in a hatchery from the eggs of wild parents.

Rainbow trout exhibited significantly higher feeding rates than brook trout, consuming nearly 4 times more food items per hour than brook trout. This disparity in food consumption was probably related to interspecific differences in mobility and aggression, but was unrelated to food preference or availability since the same number, size, and type of food items were apportioned in every match. The higher food consumption rates of rainbow trout in interspecific matches may also be attributed, in part, to interspecific differences in positioning and feeding behavior. Rainbow trout were generally distributed near the surface at about the same depth that food was introduced as drift, whereas brook trout exhibited a strong tendency to remain near the bottom. In addition, rainbow trout fed much more actively and aggressively, typically rushing to capture introduced food items and consuming them with a single bite. In contrast, brook trout tended to feed more passively, allowing food items to drift close before consuming them. These distinct vertical segregation and feeding behavior patterns clearly conferred a significant feeding advantage to rainbow trout in our study.

Under our environmental conditions, rainbow trout were generally more mobile and aggressive, and consumed more food items than brook trout. Rainbow trout accounted for 56%, 80%, and 73% of the total movements, nips delivered, and food items consumed, respectively, in paired encounters. Rainbows changed positions, nipped, and consumed food items at an average rate of 1.3, 4.0, and 2.4 times per hour, respectively, more frequently than brook trout.

These relatively distinct species-specific differences in mobility and aggression correspond closely to those observed by Newman (1956). He noted

that rainbow trout roamed more randomly and nipped more frequently than similar-sized brook trout during intraspecific and interspecific matches in standing water aquaria. Additional comparative behavioral studies are unavailable, but reported interactions of these species with other salmonids provide evidence of similar trends. Noakes (1980) reported lower mobility and aggression in young brook trout than arctic charr (*Salvelinus alpinus*) when these species were compared as intraspecific groups in aquaria. Griffith (1972) found that juvenile cutthroat trout (*Salmo clarki*) were more aggressive and dominated equal-size brook trout in laboratory stream channels. Nilsson and Northcote (1981) observed that wild, adult rainbow trout were consistently more aggressive than cutthroat trout both inter- and intraspecifically in holding tanks.

The frequency of aggressive interactions in salmonids may vary widely depending on a number of environmental factors, particularly water temperature and velocity (Kalleberg 1958, Keenleyside 1962, Hartman 1965), light intensity (Stringer and Hoar 1955), density (Newman 1956, Kalleberg 1958, Chapman 1962), and prey abundance (Newman 1956, Keenleyside and Yamamoto 1962, Symons 1968, Slaney and Northcote 1974). One or a combination of these factors may have resulted in the differential levels of aggression and mobility observed, but we have no evidence to suggest that either species was favored by our experimental conditions. Both species were maintained under identical thermal, flow, light, density, and feeding regimes and these conditions were similar to those that trout would encounter in nature.

Dominance-subordination Relations

Social organization between paired trout in this study was one of simple linear dominance hierarchies achieved and sustained by agonistic behavior. The defense of territories, fixed areas from which intruders are excluded by threat or attack (Brown 1975), was not observed. The occurrence of linear dominance hierarchies and the absence of strictly territorial behavior also has been reported for brook and rainbow trout in aquaria (Newman 1956), brook trout in aquaria (Noakes 1980) and stream channels (Griffith 1972), and rainbow trout in streams (Jenkins 1969). Newman (1956) reported that brook and rainbow trout in aquaria formed stable nip-right dominance hierarchies; territorial behavior was never observed in rainbow trout and only a slight territorial tendency was observed in a few brook trout. Noakes (1980) and Griffith (1972) both observed that the social structure of brook trout appeared to be a combination of linear dominance hierarchy and territoriality. Jenkins (1969) concluded that territories of adult, stream-dwelling salmonids are primarily partial territories (Greenberg 1947) that are based on stable, linear dominance hierarchies.

Dominance status was readily apparent in every paired match of our study. Rank between individuals was established shortly after a match was initiated and remained consistent throughout every match. During the initial confrontation between individuals in which rank was being contested, aggression was generally expressed by approach, frontal display, charge, nip, and chase. Once rank was established, displays were essentially eliminated from the behavioral repertoire of dominant fish and aggression was expressed primarily by approach, nip, and chase. Behavioral activities expressed by subordinate fish were restricted to flight and submissive display. After rank was established, the frequency of aggressive interactions substantially decreased with time; subordinate individuals rarely nipped dominant individuals after the first few hours of cohabitation.

Social position was not significantly influenced by the species of the experimental fish. Brook trout were dominant in 9 and rainbow trout were dominant in 5 of the 14 interspecific matches; neither species appeared to possess an innate advantage in establishing dominance. Newman (1956) reported a similar tendency for brook trout to dominate rainbow trout in aquaria, but concluded that in larger tanks neither species was more likely to dominate. Apparently aggressive superiority alone, as displayed by rainbow trout, does not always result in social superiority.

Sex had no significant role in determining rank or effect on the frequency of movements, aggression, or food consumption. Neither male nor female trout were consistently more dominant, mobile, aggressive, or successful foragers. In 10 opposite-sex matches (3 intraspecific and 7 interspecific), female trout were dominant in 6 matches and male were dominant in 4 matches. Male trout tended to be more mobile and consumed more food items, and female trout tended to be more aggressive (Table 2). Similarly, no significant relationship was measured between rank and sex with respect to mobility, aggression, and foraging ability. The only pattern emerging from

Table 2. Mean Number of Movements, Nips Delivered, and Food Items Consumed Per Hour for Paired Trout As a Function of Rank and Sex

Trout Pairings	N	Observation Time (hours)	Movements	Food Items Consumed	Nips Delivered
Rank:					
Dominant	14	218	8.8[a]	2.8[a]	3.5[a]
Subordinate	14	218	5.6	1.7	0.4
Sex:					
Male	10	218	7.5	2.5	1.6
Female	10	218	6.6	1.8	2.7

[a] Significantly larger values ($P < 0.05$).

these relationships was that subordinate male trout were generally more mobile, aggressive, and successful foragers than subordinate female trout. On the basis of our observations it appeared that either sex may achieve social dominance or be more mobile, aggressive, or successful foragers. Newman (1956) and Jenkins (1969) also reported no evidence of sexual superiority in the establishment of dominance among brook or rainbow trout.

Social status had a significant effect on the mean number of movements, nips delivered, and food items consumed. Dominant trout, regardless of species, sex, or size, were more active ($P < 0.01$), more aggressive ($P < 0.01$), and consumed more food items ($P < 0.05$) than subordinates (Table 2). Dominant trout altered positions, nipped, and consumed food items an average of 1.6, 8.8, and 1.7 times per hour, respectively, more frequently than subordinate trout. Subordinate individuals were generally restricted to the downstream section of the observation area and their upstream foraging activities often elicited aggression and activity by dominant fish. Since food was intentionally introduced at the upstream inlet to stimulate stream drift, dominant fish had virtually unrestricted first access to the food items. Dominant trout accounted for 61% of the total movements, 89% of the total nips delivered, and 62% of the total food items consumed. Dominance in this study, as has been observed in other salmonids (Chapman 1962, Fenderson et al. 1968), clearly conferred an advantage in mobility, aggression, and food consumption.

Conclusions

Under our laboratory conditions, wild, adult rainbow trout were more mobile, aggressive, and successful as foragers on drifting prey than similar-sized brook trout. However, neither species was competitively superior in establishing social dominance or excluding interspecific rivals. Long-term field investigations examining behavioral interactions, resource partitioning, population dynamics, and environmental factors are needed to clarify the mechanisms responsible for the altered distributions of brook and rainbow trout in the southeastern United States.

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