Environmental influences on territoriality of juvenile brook charr, *Salvelinus fontinalis*, in a stream environment

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Synopsis

Juvenile brook charr, *Salvelinus fontinalis*, defending territories in a laboratory stream channel changed their defensive tactics when fish numbers or water current velocity were increased. The associated increase in energy costs of territorial defense were apparently reduced by using relatively more lateral displays and fewer chases to repel intruders, and by decreasing territory size. Territory size tended to increase with food ration, although levels of aggression were not affected. These results emphasize the importance of energetic considerations in territoral defense in these fish, and are discussed in terms of current hypotheses regarding the resource base for territoriality.

Introduction

Brook charr alevins, *Salvelinus fontinalis*, begin defending territories shortly after emerging from the gravel stream bed (Noakes 1980). The shape of their territories (Noakes & McNicol 1982) and their defense (McNicol & Noakes 1981) support the hypothesis that territorial defense is determined by energetic costs and benefits (Davies 1978, Dill 1978a). How they respond to changes in costs and benefits of defense should therefore test this hypothesis. Territoriality in these fish appears to be food based (Dill 1978a, McNicol & Noakes 1981) so any change in habitat quality that alters territoriality would presumably affect growth and survival (and hence, ultimately, fitness). Furthermore, total production in brook charr populations is directly related to that of age 0 fish (Carline 1977), so

behavioural alterations could also have significant repercussions at the population or community level.

Feeding territories have been the subject of considerable recent interest (Verner 1977, Dill 1978a, Ebersole 1980, Hixon 1980). However, previous studies of these in salmonids have been somewhat limited, with conflicting results (see Cole & Noakes 1980). Some studies have shown a decrease in territorial aggression and size of territories with an increase in food (Symons 1968, Slaney & Northcote 1974, Mason 1976), but others have found no change in these measures with changes in food supply (Symons 1971, Dill 1978b). Our study was designed to determine how changes in water current velocity, fish numbers (density) and food ration affect territory size and shape, as well as levels of agonistic behaviour in juvenile brook charr. These variables can show either short or long term variations in a stream environment, and affect behavior in salmonids.

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Materials and methods

Experiment I

Our brook charr originated from a self-sustaining population in the headwaters of Sheldon Creek, a tributary of the Nottawasaga River, Ontario. Eggs were collected and inseminated there, then held and reared in our laboratory as previously described (McNicol & Noakes 1981). Fish used in observations were about 4 months old and ranged from 38 to 53 mm total length (mean 46 mm) and from 0.36 to 1.06 g (mean 0.68 g) live weight, respectively. One week prior to, and during experimentation they were fed a daily ration of 0.6% (dry weight of food to live body weight) at 1630 hours.

Fish were observed in four plexiglass enclosures (0.6 wide × 0.4 m high) with nylon screening (1.6 mm mesh) placed 0.7 m apart as upstream and downstream barriers. Colored glass marbles at 5 cm intervals (10 per column, 13 per row) level with a uniform layer of light-colored aquarium gravel provided a rapid means of accurate plotting of fish positions. Two enclosures were placed in each of two channels (5 × 1.3 × 0.5 m deep) of a large (~12000 l) laboratory stream tank (details in McNicol 1979). Feeding was accomplished through three plastic tubes in front of the upstream barrier of each enclosure (McNicol & Noakes 1981). Fish were fed commercial trout food (Number 2 trout chow, Martin's Feed Mill, Elmira, Ontario) 0.8–1.0 mm diameter pellets (0.017–0.02 particle-size to fish-length ratio). Proximate composition of this food is given by Leatherland et al. (1977). Opaque, black polythene sheeting behind the feeding tubes and over the glass windows of the stream tank minimized disturbance to the fish. Viewing ports directly in front of each enclosure allowed for behavioral observations. Incandescent bulbs above the enclosures provided similar total illumination (0.03 watts cm^{-2}; R413 Pyranometer) at the gravel surface of all four enclosures at all current velocities tested. Water temperature was maintained at 14 ± 1°C at a depth of 23 cm by replacing about 20 l min^{-1} of filtered well water. Water temperature was uniform throughout all enclosures as a result of flow, and mixing at the upstream and downstream ends of each channel.

This experiment simultaneously tested the effects of four different water current velocities (5.5., 11.0, 16.0 and 23.0 cm s^{-1} at mid water depth) and four fish densities (10, 15, 20 and 25 fish per enclosure) on levels of aggression and territorial size. All four densities were tested at the same time at one randomly selected water velocity. Water velocity varied only about 10% between midwater and substrate positions in each enclosure for any given velocity. This constituted one treatment. Twenty-four hours prior to a treatment, 20 fish were chosen as randomly as possible from the holding tank, anesthetized (75 mg l^{-1}, MS-222. Syndell), weighed and measured (total length), then returned to the holding tank and allowed 24 hours to recover. Following this, fish were taken from the holding tank in groups of five and randomly assigned to one of the four enclosures until the density to be tested in each (randomly assigned) was reached. This required a total of 70 fish.

After a 48 h familiarization period in the enclosure, observations were made over the next 48 h. Fish were then removed from the enclosures and returned to the holding tank. The following day the same procedure was repeated for the next randomly chosen treatment until all four velocities had been tested (velocity profiles were similar among enclosures at any given velocity). Another replicate of each treatment was performed in random order. All four densities were again assigned to the enclosures at each velocity with the restriction that a density tested in one channel during the first replicate was randomly assigned to one of the two enclosures in the other channel for the second replicate, thus taking into account possible channel effects.

On each observation day enclosures were observed in random order between 0900 and 1400 hours. There was no apparent difference in activity of the fish throughout this period. During this time two types of measurements were made: frequencies and durations of specific agonistic acts and associated events, and plotting of points of interaction between fish.

Five focal fish were randomly selected from each enclosure (Altmann 1974). As far as possible, different individuals were observed in successive obser-

vations. Fish were individually marked by caudal and dorsal fin branding in conjunction with adipose fin clips (McNicol & Noakes 1979). Each was observed for a continuous five-minute period during which the occurrence and durations of certain behavioral patterns were recorded on a multi-channel event recorder (Esterline-Angus A620X, chart speed 7.6 cm min^{-1}) connected to a manual keyboard. Frequencies of five distinct agonistic activities, lateral display (LD), charge (CHG), chase (CHS), headturn (HT) and nip (NP), were recorded. Durations of LD and CHS were also recorded. LD, CHG and CHS (in order of increasing aggressive nature) were as previously described (McNicol & Noakes 1981). HT occurred when the aggressor, positioned laterally to a conspecific (usually during LD), would suddenly bend its head towards the conspecific at an angle of about 30–40°. This event was of short duration and sometimes occurred a number of times during the same encounter. Often it was followed by NP, which was a rapid biting by one fish of any part of another (usually the tail). Also recorded was the total time each fish spent holding a stationary position within 5 cm of the bottom.

In addition to these measurements, the number of fish within 5 cm of the bottom was recorded at the beginning and end of observations at each enclosure. Also while event frequencies were being recorded, it was noted which fish were actively defending territories. When frequency measurements were complete on all five fish, the territorial fish noted earlier were scanned simultaneously (Altmann 1974) for a half-hour period. During this time, the primary station (that station where a territorial fish usually positioned itself to defend a territory) of each was plotted. Also plotted were the points where intruding fish evoked CHG reactions by a resident fish stationed at its primary station. Distances were later measured between these points of interaction (represented by that part of the intruder closest to the resident) and the primary station (represented by the anterior end of the resident). Mean interaction distances were later calculated for the front 90° quadrant, and side 90° quadrants (combined) to provide a measure of territory size.

Data were analyzed using the split-plot Anova (Steel & Torrie 1960). Current velocities were considered the whole plot and fish densities the split-plot treatments. Each replicate (one in each channel) represented a block such that any channel effects could be eliminated as a source of error. If the computed F value for interaction effects was less than one, its sum of squares was pooled with that of the split-plot (fish density) treatment. The computed F value for fish density treatments was then recalculated using this pooled sum of squares (Afifi & Azen 1972).

To eliminate variability introduced when absolute frequencies of aggressive and non-aggressive fish are combined for analysis, relative frequencies were computed and analyzed in addition to absolute measures. These were computed as the ratios of each activity to total frequency of activities (sum of all agonistic activities), total frequency of encounters (LD + CHG + CHS), LD + activity, and CHG + activity. Due to the number of zero values recorded for other activities, no other ratios could be computed. No agonistic activities were observed during one treatment replicate. To eliminate this zero value for ratio computation, it was treated as a missing value and a number generated (Steel & Torrie 1960) to allow analysis. All percentage and ratio data were given an arcsine square root transformation ($x^1 = $ arcsine $\sqrt{x}$) before analysis. The data were transformed because of non-normality and non-homogeneity of variance. This transformation was judged most appropriate by residual analysis and normal probability plots. Any means plotted from such data were derived by applying a reverse transformation to the transformed means.

Experiment II

This experiment determined the effect of current velocity on territory size, shape and structure. Experiment I had been designed to give similar though less detailed information. However, a possible confounding factor became evident in that fewer fish remained on the bottom at the lower velocities tested (5.5 and 11 cm s^{-1}) than at the higher velocities. This experiment was thus designed, in part, to verify results from the first experi-

ment by testing at current velocities (14.5, 17.5, 23.5 and 28.5 cm s^{-1}) at which all fish remained on bottom.

Charr eggs from the previously described source were treated as before, and then three weeks after hatching, 1000 fish were transferred to a circular fibreglass tank, and held and fed as in Experiment 1. Fish were observed in one of the previously described enclosures, with the barrier screens moved farther apart, providing a viewing area of 2.0 × 0.55 m. Incident light, water temperature and replacement rates were as before.

Six days prior to the experiment, 20 fish were selected as those individuals showing territorial defense in preliminary observations. These were approximately 5 months old, and ranged from 41–33 mm total length (mean 47 mm) and 0.48–1.14 g live weight (mean 0.74 g), respectively. During the following recovery week and throughout the experiment, they were fed a daily ration of trout chow at 1630 h (type, amount and manner as before). After the recovery period the fish were placed into the enclosure (current speed 17.5 cm s^{-1}) and allowed 2 days' accommodation. The following day, the first current velocity was randomly selected and the fish allowed a further 40 h accommodation to adjust to the conditions in the observation tank.

Observations were made daily (0900–1200 hours, 1300–1600 hours) over the next 3 days. The stations of those fish actively defending territories were plotted as well as the positions of intruders evoking either CHS or CHG responses from these fish as recorded by direct observation and video recording (McNicol & Noakes 1981). When current velocities were changed the water flow was interrupted for a 10 minute period. Fish did not appear to be greatly disturbed by this and most territorial fish returned almost immediately to their original stations once water flow was resumed. Forty hours accommodation was allowed before observations were taken at the new current velocity. The fish were weighed and measured following the experiment.

From these observations, mean interaction distances were computed for front and side quadrants. For each current velocity, stations from which a fish defended a territory were superimposed and the points of interaction around each plotted together.

Territory size was then computed as the polygonal area enclosed by joining the outermost interaction points.

Data were analyzed using Friedman's two-way analysis of variance (Siegel 1956) with each fish considered a block. Treatment means were compared using the sign test (Siegel 1956).

Experiment III

The same fish used in Experiment II were used in this one but with five replacements (four were too emaciated, and one too large). Total lengths and weights of all 20 were 38–54 mm (mean 46 mm) and 0.38–1.16 g (mean 0.68 g), respectively.

Three ration sizes were tested: 0.5, 1.0 and 2.0% dry weight to live body weight per day of the previously described trout chow, based on the mean weight of the 20 fish. These fish were placed into the same enclosure used in the previous experiment (mid-water current velocity, 25 cm s^{-1}) with water temperature and replacement rate as before. For the next 2 days they were fed at one test ration (randomly chosen), half at 0830 hours and the other half at 1230 hours. This was followed by 4 days of observations (feeding times and ration same as previous 2 days) and one day food deprivation before the next ration was tested. The fish were weighed and measured following the last day's observation.

On the first, third and fourth days of observation, recordings were made between 0930 and 1230 hours, and 1330 and 1630 hours (allowing one hour between feeding and the commencement of observations). During this time territory plotting was accomplished by direct and video camera observations, as previously described, for fish holding stable territories. Mean interaction distances and total territory size were computed as before.

On the second day of observation, frequencies of agonistic acts and the amount of time spent station-holding by each fish were recorded using the event recorder. Recordings were made between 0930 and 1230 hours, and 1330 and 1630 hours. During each of these periods, each of the 20 fish was observed in a random sequence for 7 min (280 min total). The occurrence of LD, HT, CHG, CHS, NP and frontal

displays were recorded. Frontal displays (FD) were similar to those described for other salmonids (e.g. Keenleyside & Yamamoto 1962). During FD the dorsal surface of the fish was slightly arched in a convex manner with the pectoral, ventral and anal fins extended while the dorsal fin was depressed. The branchiostegal membranes were lowered in the same fashion as occurred during LD. The displaying fish usually faced the intruder and would move towards it while displaying.

Data were analyzed using Friedman's two-way analysis of variance (Siegel 1956).

Results

Experiment 1

Although a statistically significant increase (2 mm) in average total length occurred by the end of this experiment, its effect was assumed to be insignificant within the range and variability in readings between individuals (Table 1). No significant interactions between current velocity and fish density effects occurred in those analyses showing significant current velocity and/or fish density trends.

Table 1. Effect of current velocity and fish density on mean absolute frequencies of agonistic activities for 10 fish (range in parentheses) over a five minute period.

Current velocity (cm s^{-1})	Fish density	% Time stationary on bottom	Agonistic activity[1]					Frequency of encounters	Total frequency
			LD	HT	CHG	CHS	NP		
5.5	10	62.0(37.7–82.8)	0.6(0–3)	0.5(0–3)	1.1(0–4)	0.5(0–2)	0	2.2(0–8)	2.7(0–11)
		80.4(54.6–100)	0.6(0–5)	0.3(0–3)	1.7(0–7)	0.8(0–3)	0	3.1(0–15)	3.4(0–18)
	15	81.2(69.7–95.0)	0.1(0–1)	0.1(0–1)	1.7(0–9)	0.4(0–3)	0	2.2(0–9)	2.3(0–9)
		78.6(51.8–90.3)	0.6(0–2)	0.3(0–2)	2.6(0–4)	0.5(0–3)	0.5(0–2)	3.7(0–7)	4.5(0–8)
	20	74.5(20.8–98.3)	0.3(0–2)	0.1(0–1)	1.8(0–8)	0.1(0–1)	0.2(0–1)	2.2(0–10)	2.5(0–20)
		84.7(56.7–99.0)	0.2(0–1)	0.4(0–2)	1.1(0–9)	0.5(0–5)	0.3(0–3)	1.8(0–15)	2.5(0–11)
	25	65.3(31.7–90.9)	1.0(0–3)	0.1(0–1)	1.9(0–6)	0.2(0–2)	0.3(0–2)	3.1(0–8)	3.5(0–10)
		81.1(92.2–48.1)	0.2(0–1)	0	0.6(0–4)	0.1(0–1)	0.2(0–1)	0.9(0–6)	1.1(0–7)
11	10	79.4(44.0–100)	0.4(0–1)	0.1(0–1)	1.8(0–8)	0.4(0–3)	0.2(0–1)	2.6(0–11)	2.9(0–11)
		80.6(42.5–96.4)	0.1(0–1)	0	1.0(0–3)	0.2(0–1)	0.4(0–2)	1.3(0–3)	1.7(0–5)
	15	85.7(60.8–100)	0.6(0–4)	0.6(0–5)	1.7(0–8)	0.3(0–2)	0.5(0–3)	2.6(0–10)	3.7(0–15)
		85.9(61.7–100)	0.3(0–1)	0	1.2(0–5)	0.3(0–1)	0.4(0–3)	1.8(0–7)	2.2(0–10)
	20	89.4(73.2–99.7)	1.3(0.9)	0.1(0–1)	1.9(0–7)	0.2(0–1)	0.1(0–1)	3.4(0–17)	3.6(0–18)
		79.9(61.5–94.0)	0.3(0–2)	0.2(0–2)	1.0(0–5)	0.1(0–1)	0.1(0–1)	1.4(0–6)	1.7(0–7)
	25	94.1(88.0–97.6)	0.4(0–3)	0.4(0–4)	0.3(0–4)	0	0.2(0–1)	1.3(0–7)	1.9(0–12)
		87.5(57.4–99.7)	0.2(0–1)	0	0.9(0–3)	0.1(0–1)	0.2(0–2)	1.2(0–4)	1.4(0–6)
16	10	78.3(36.2–100)	0.4(0–3)	0.1(0–1)	2.0(0–6)	0.5(0–3)	0.5(0–4)	2.9(0–9)	3.5(0–12)
		89.1(71.3–97.3)	0.3(0–2)	0	0.5(0–4)	0	0	0.8(0–6)	0.8(0–6)
	15	83.4(32.3–99.7)	1.4(0–7)	0.3(0–3)	1.9(0–9)	0.3(0–1)	0.3(0–2)	3.6(0–17)	4.2(0–22)
		86.8(71.70–94.2)	0.4(0–3)	0.2(0–2)	0.6(0–2)	0	0.1(0–1)	1.0(0–4)	1.3(0–7)
	20	76.7(60.5–98.0)	2.0(0–8)	0.2(0–1)	1.9(0–5)	0	0.7(0–3)	3.9(0–12)	4.8(0–13)
		91.8(71.7–99.0)	0.2(0–1)	0	0.7(0–3)	0.1(0–1)	0.1(0–1)	1.0(0–4)	1.1(0–4)
	25	92.8(81.6–100)	0.7(0–5)	0	0.3(0–2)	0	0.1(0–1)	1.0(0–5)	1.1(0–5)
		86.0(64.6–100)	0.6(0–2)	0.2(0–1)	0.2(0–1)	0.1(0–1)	0.1(0–1)	0.9(0–4)	1.2(0–4)
23	10	93.6(82.0–100)	0.1(0–1)	0	0.4(0–4)	0.2(0–2)	0.2(0–2)	0.7(0–6)	0.9(0–8)
		94.9(84.0–100)	0	0	0	0	0	0	0
	15	94.9(71.4–100)	0.4(0–3)	0.2(0–2)	0.4(0–4)	0	0.3(0–3)	0.8(0–7)	1.3(0–12)
		85.5(46.7–100)	0.3(0–2)	0.2(0–2)	0.1(0–1)	0	0.1(0–1)	0.4(0–2)	0.7(0–5)
	20	93.3(75.7–100)	0.3(0–2)	0	1.0(0–7)	0.2(0–1)	0.1(0–1)	1.5(0–8)	1.6(0–9)
		95.1(75.6–100)	0.6(0–4)	0.7(0–5)	0.4(0–2)	0.2(0–1)	0.2(0–1)	1.2(0–7)	2.1(0–13)
	25	92.1(70.5–100)	0.2(0–1)	0	0.1(0–1)	0	0.1(0–1)	0.3(0–1)	0.4(0–2)
		86.7(43.0–99.7)	0.3(0–3)	0.2(0–2)	0.9(0–5)	0.1(0–1)	0.2(0–2)	1.3(0–5)	1.7(0–9)

[1] LD = lateral display, HT = head turn, CHG = charge, CHS = chase, NP = nip.

Table 2. Summary of current velocity (V) and fish density (D) effects on relative (A:B) frequencies of agonistic activities.

		A									
		LD		HT		CHG		CHS		NP	
		V	D	V	D	V	D	V	D	V	D
B	Total frequency	↑^{5}	↑^{10}	NS	NS	NS	NS	↓^{5}	↓^{10}	NS	NS
	Frequency of encounters	↑^{5}	↑^{10}	NS	NS	↓^{10}	NS	↓^{5}	↓^{10}	NS	NS
	LD + A	–	–	NS	NS	–	–	↓^{10}	↓^{10}	NS	NS
	CHG + A	↑^{5}	NS	NS	NS	–	–	↓^{5}	NS	NS	NS

(↑^{x} and ↓^{x} indicate increasing and decreasing trends, respectively, with increasing V or D at the overall 'x' percentile level of significance. NS, no significant trend. –, no test performed. Abbreviations as in Table 1).

Absolute frequencies of LD, CHG, HT and NP showed no significant trends. However, CHS decreased significantly ($0.01 < p < 0.05$) with increasing fish density (Table 1). No significant trends were apparent with total frequencies of activities or total frequency of encounters.

The results of relative frequency analyses are summarized in Table 2. In general, as current velocity increased, LD tended to increase and CHS decrease relative to other activities (Fig. 1). The same trend, though only significant at $0.05 < p < 0.10$, occurred in relation to increasing fish density (Fig. 2). However, in all cases where such a level of significance occurred, the high and low density means were significantly different from each other at $0.01 < p < 0.05$.

As current velocity increased, the amount of time spent stationary on bottom increased significantly ($0.01 < p < 0.05$) (Table 2). However, no change in activity was evident with increasing fish density.

Mean duration of LD showed no trends with current velocity or fish density. CHS interactions were too few throughout all replicates for analysis.

Only CHG to the side occurred frequently enough to establish interaction distances for each territorial fish of each treatment replicate. As fish density increased, mean side CHG interaction distance significantly ($p < 0.01$) decreased (Table 3). This decrease was greatest between densities of 10 and 15 fish (Fig. 3). No trend was evident with increasing current velocity in either analysis.

Mean front CHG interaction distance also decreased with increasing fish density ($0.01 < p < 0.05$), although 10 of the 16 treatment means were derived from replicates for which only one or two observations were available (Table 3). A non-significant ($0.05 < p < 0.10$) inverse relationship between front CHG interaction distance and current velocity was also evident, with the mean distance at 5.5 cm s^{-1} being significantly greater ($0.01 < p < 0.05$) than those at the other three velocities.

Experiment II

Seven of the 20 experimental fish held stable territories throughout the experiment, during which time no significant growth occurred. None of the territorial fish remained at the same station throughout all four current velocities. Whether this was a result of the disturbance of changing velocities or whether it represented a natural tendency to periodically shift territory sites was not clear. To overcome this difficulty when comparing treatment effects, all stations from which a fish defended a territory with five or more interactions were combined and plotted for each velocity. Stations of any one fish tended to be in the same vicinity of the enclosure and thus in similar proximity to neighbouring territorial fish and enclosure walls (which tended to compress territories). The same considerations were made when grouping measurements from each fish for comparison across current velocity treatments. Measurements for some fish were not frequent enough or could not be compared in all directions across all current velocities, and were therefore excluded from the analysis.

Mean side CHG interaction distances tended to decrease with increasing current velocity ($0.01 <$
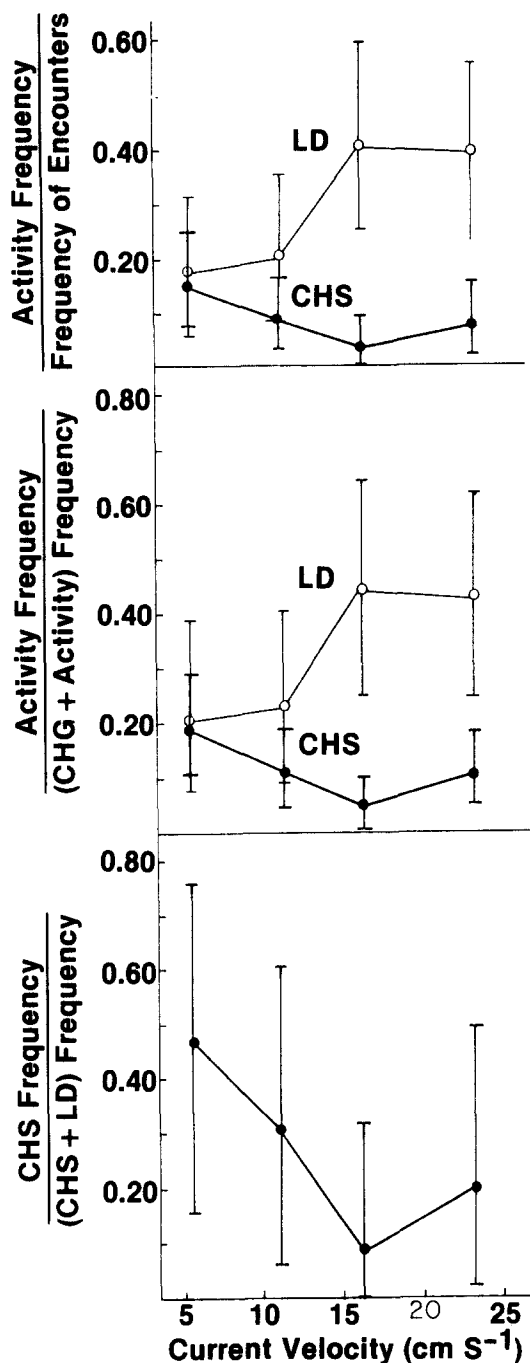
Fig. 1. Effect of current velocity on mean ratios of lateral display (LD) and chase (CHS) frequencies to frequencies of other activities (over all fish densities; 95% confidence intervals indicated).
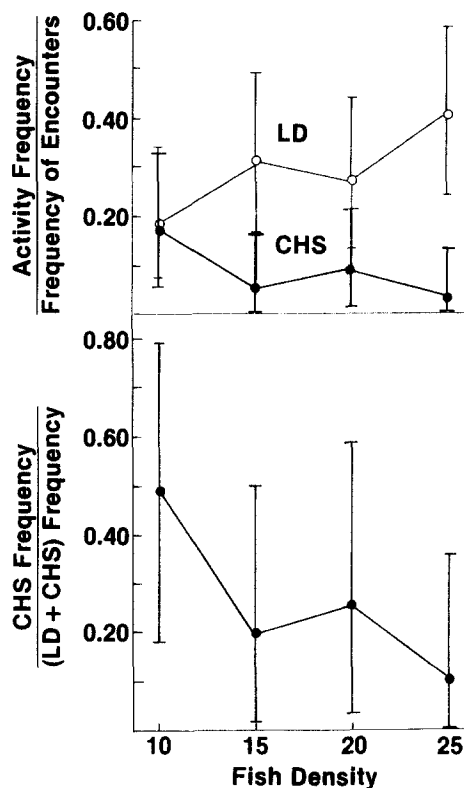

Fig. 2. Effect of fish density on mean ratios of lateral display (LD) and chase (CHS) frequencies to frequencies of other activities (over all current velocities; 95% confidence intervals indicated).

$p < 0.05$), although this trend was not consistent for all fish (Table 4). No significant trend occurred among side CHS interactions. Comparisons of front interaction distances were only possible for two fish. Both showed a statistically non-significant tendency towards having larger mean interaction distances at the lowest current velocity (Table 4). No significant trend was evident with territory area.

Typical cardioid territories (McNicol & Noakes 1981, Noakes & McNicol 1982) were defended at all current velocities tested, though no apparent relationship between territory shape and current velocity was evident from territory plots. Ratios of CHG to CHS interaction distances to the front and side were calculated and analyzed to determine if the outer region of a territory (where CHG predominates, see McNicol & Noakes 1981) was compressed more or less than the inner region (where CHS

Table 3. Effect of fish density and current velocity on mean side and front CHG (charge) interaction distance (cm). Sample size in parentheses.

Fish density	Current velocity (cm s^{-1})							
	5.5		11.0		16		23	
	Front	Side	Front	Side	Front	Side	Front	Side
10	14.0(1)	20.0(5)	12.3(3)	13.3(7)	10.5(2)	13.8(4)	7.0(1)	18.0(4)
	19.0(1)	11.3(6)	10.7(3)	11.6(8)	9.7(3)	11.1(7)	11.0(1)	11.7(3)
15	15.0(1)	11.4(7)	8.0(1)	10.9(9)	5.0(1)	10.6(5)	9.0(2)	7.9(8)
	10.0(1)	8.9(7)	10.5(4)	7.9(8)	8.5(2)	10.2(6)	8.5(2)	8.5(6)
20	9.0(2)	9.6(7)	11.3(4)	9.7(9)	8.5(4)	9.0(6)	9.7(3)	8.5(6)
	12.7(4)	11.2(5)	9.7(3)	8.0(10)	8.5(4)	8.7(10)	8.0(1)	9.4(9)
25	7.0(1)	7.8(8)	8.67)	8.7(7)	7.5(4)	6.2(6)	12.0(3)	8.8(11)
	7.0(2)	7.1(7)	6.7(3)	7.6(8)	9.0(4)	8.6(5)	9.0(7)	9.2(10)

predominates) when subjected to increasing current velocities. No trend was apparent (Table 4) in either direction (again, only two fish could be used in the comparison).

Experiment III

No significant growth occurred among the 20 fish, but the seven which held stable territories throughout the experiment showed an average length and weight increase of 3 mm and 0.22 g, respectively. This growth was considered to have had minimal effects on results, especially since treatments were randomized.

Absolute frequencies of each agonistic activity, total frequencies of agonistic activities, and frequency of encounters (LD + CHG + CHS + FD) showed no significant change with ration size. Relative frequencies of each event (except HT and FD, which were too infrequent) to total frequency and frequency of encounters also failed to show a significant ration effect, as did frequencies of CHG, CHS and LD relative to one another. Duration of LD and CHS, and percent time station-holding also did not change. This was the case when separate analyses were performed on territorial and non-territorial fish, as well as both groups combined.

As in the previous experiment, few territorial fish remained at the same station through all three

treatments, although the stations occupied by any one fish were located in the same vicinity of the enclosure. Stations were grouped and compared across treatments as previously described.

Mean front CHG interaction distances were significantly greater ($0.01 < p < 0.05$) at the 2% ration than at the lower rations (Table 5). No other significant trends were apparent among other interaction distances, or with total territory size.

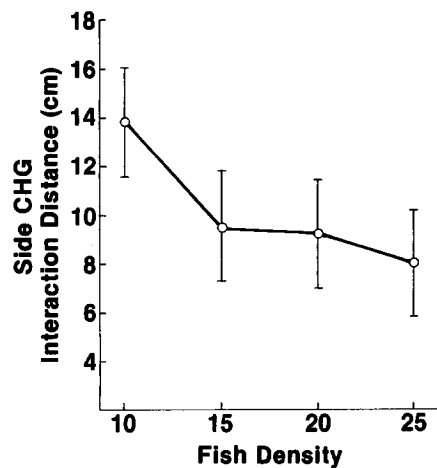Cardioid territories were defended at all ration

Fig. 3. Effect of fish density on mean side charge (CHG) interaction distances (over all current velocities; 95% confidence intervals indicated).

levels. Front to side CHS interaction distance were significantly different (0.01 < p < 0.05) among the three ration levels (Table 5). Although this trend did not appear to be linear, ratios were greatest at the higher ration level for three of the four fish for which such ratios could be calculated, indicating an elongation of the territory in the upstream direction. No obvious change in scatter of interaction points was observed among territorial fish across ration levels. CHG to CHS interaction distance ratios to the front and side did not change significantly with ration level.

Discussion

When exposed to the directional force of flowing water juvenile brook charr defend their territories in a manner indicative of energy cost efficiency (McNicol & Noakes 1981). As we predicted, raising the costs of territory defense by increasing water current velocity or fish density resulted in compensatory changes in defense tactics. With greater fish numbers, territory defense costs should increase as more intruders impinge on a territory. One response by brook charr to reduce such increases

Table 4. Effect of current velocity on mean interaction distances and their ratios, and territory size of individual territorial fish (F, front; S, side. The number of interactions is given in parentheses. –, no measurements were obtained. Abbreviations as in Table 1).

Fish No.	Current velocity (cm S^{-1})	Mean interaction distances (cm)				Mean ratios of interaction distances				Territory size (cm^2)
		F. CHG	F. CHS	S. CHG	S. CHS	F. CHG/CHS	S. CHG/CHS	CHG F./S.	CHS F./S.	
10	14.5	–	–	9.0(22)	7.4(12)	–	1.22	...	–	216)
	17.5	–	–	8.0(8)	8.3(7)	–	0.96	–	–	262
	23.5	–	–	11.4(17)	5.3(3)	–	2.15	–	–	335
	28.5	–	–	8.5(8)	8.0(2)	–	1.06	–	...	334
13	14.5	27.0(7)	20.0(22)	15.6(14)	12.3(14)	1.35	1.27	1.73	1.63	1071
	17.5	18.4(16)	15.6(30)	11.7(19)	12.0(12)	1.18	0.98	1.57	1.30	734
	23.5	20.2(19)	13.8(28)	14.6(22)	12.9(21)	1.46)	1.13	1.38	1.07	843
	28.5	28.1(9)	14.5(23)	14.2(6)	10.0(13)	1.70	1.42	1.98	1.65	795
14	14.5	–	–	16.6(9)	10.1(10)	–	1.64	–	–	496
	17.5	–	–	13.0(12)	11.8(13)	–	1.10	–	...	656
	23.5	...	–	11.3(4)	9.6(5)	–	1.18)	–	–	209
	28.5	–	–	10.3(15)	8.7(11)	–	1.18	–	...	485
15	14.5	–	...	18.0(6)	16.8(24)	–	1.07	–	–	1470
	17.5	–	–	17.5(2)	14.7(6)	–	1.19	–	–	1489
	23.5	...	–	21.2(18)	20.8(10)	...	1.02	...	–	1972
	28.5	–	–	16.7(13)	19.2(6)	–	0.87	–	...	1762
16	14.5	–	–	17.6(12)	10.6(19)	–	1.66	–	...	1469
	17.5	...	–	11.3(18)	7.9(17)	–	1.43	...	–	638
	23.5	–	...	11.8(5)	9.9(9)	–	1.19	–	–	362
	28.5	–	–	7.7(7)	6.2(11)	–	1.24	–	–	274
19	14.5	22.4(7)	18.6(18)	26.8(8)	22.1(48)	1.20	1.21	0.84	0.84	1787
	17.5	18.2(55)	16.5(20)	25.9(27)	21.0(30)	1.10	1.23	0.70	0.79	1484
	23.5	17.6(14)	13.0(8)	12.6(8)	11.9(7)	1.35	1.06	1.40	1.09	504
	28.5	15.8(17)	14.6(17)	18.4(30)	16.3(23)	1.08	1.13	0.86	0.90	915
23	14.5	–	–	11.8(5)	8.6(17)	–	1.37	–	–	517
	17.5	–	–	9.3(3)	9.0(1)	...	1.03	–	...	164
	23.5	–	–	9.9(15)	8.8(4)	–	1.13	–	–	349
	28.5	–	–	14.6(7)	10.0(6)	–	1.46	–	–	542

Table 5. Effect of ration size on mean interaction distances and their ratios, and territory size of individual territorial fish. Abbreviations as in Table 1 and 4.

Fish number	Ration size (% body wt. per day)	Mean interaction distances (cm)				Mean ratios of interaction distances				Territory size (cm²)
		F. CHG	S. CHG	F. CHS	S. CHS	F. CHG/CHS	S. CHG/CHS	F./S. CHG	F./S. CHS	
2	0.5	17.1(13)	12.7(15)	14.7(6)	14.2(12)	1.16	0.89	1.35	1.04	836
	1.0	19.8(4)	23.0(22)	17.5(2)	26.2(11)	1.13	0.88	0.86	0.67	1235
	2.0	24.0(16)	14.2(25)	17.1(14)	11.6(12)	1.40	1.22	1.69	1.47	821
10	0.5	–	10.0(24)	–	12.7(7)	–	0.79	–	–	766
	1.0	–	11.7(13)	–	10.2(11)	–	1.15	–	–	781
	2.0	–	12.5(16)	–	10.0(9)	–	1.25	–	–	787
13	0.5	16.1(25)	10.1(18)	12.7(14)	9.0(7)	1.27	1.12	1.59	1.41	575
	1.0	12.8(17)	9.3(16)	11.7(14)	9.1(16)	1.09	1.02	1.38	1.29	247
	2.0	20.2(10)	14.4(13)	13.6(25)	8.8(15)	1.49	1.64	1.40	1.55	882
15	0.5	–	24.2(24)	–	22.1(54)	–	1.10	–	–	1553
	1.0	–	22.9(37)	–	21.2(28)	–	1.08			1456
	2.0	–	17.0(22)	–	13.4(13)	–	1.27	–	–	1001
16	0.5	19.0(15)	18.2(5)	13.7(20)	15.3(3)	1.39	1.19	1.04	0.90	737
	1.0	18.4(24)	17.2(16)	13.4(33)	15.0(26)	1.37	1.15	1.07	0.89	852
	2.0	26.5(14)	19.6(20)	20.8(19)	18.3(22)	1.27	1.07	1.35	1.14	1254
19	0.5	18.3(6)	22.4(12)	16.6(11)	17.5(27)	1.10	1.28	0.82	0.95	1075
	1.0	16.1(28)	21.5(28)	14.1(26)	20.9(35)	1.16	1.08	0.76	0.67	1545
	2.0	23.1(20)	24.8(16)	19.1(29)	21.9(27)	1.21	1.13	0.93	0.87	1947
23	0.5	–	13.6(26)	–	8.2(5)	–	1.66	–	–	807
	1.0	–	13.5(17)	–	12.4(5)	–	1.09	–	–	390
	2.0	–	10.9(26)	–	10.2(10)	–	1.07	–	–	308

was to use apparently less energetically costly agonistic activities (see McNicol & Noakes 1981) in greater proportions to repel intruders. Young rainbow trout (*Salmo gairdneri*) similarly respond to increased fish density by reducing overt agonistic actions and increasing threat displays (Cole & Noakes 1980).

The other response by brook charr was to decrease territory size. This response has also been reported among juvenile rainbow trout (Cole & Noakes 1980) and Atlantic salmon, *Salmo salar* (Kalleberg 1958). This agrees with the predictions of Dill's (1978a) model of feeding territories, which assumes that the territory holder maintains an optimal territory size, maximizing net energy intake (energy maximizer, Schoener 1971). Territory size is reduced to maintain the maximum net energy return from the territory, i.e. giving up some energy intake (feeding territory) but reducing energy (de-

fense) costs by a greater amount. Such a reduction in territory size may explain why no significant increase in number of agonistic encounters occurred with increasing density. Hixon's (1980) model for contiguous territories predicts that with decreasing food availability, territory size might first increase, then remain constant, assuming that the initial territory size had been forced to contract below the optimum size for non-contiguous territories under these conditions.

With increasing water current velocity, each feeding foray or intruder expulsion by a territorial resident becomes increasingly expensive energetically. Juvenile brook charr, as would be predicted, spent less time moving over the substrate and more time at their stations as current velocity increased. Fewer contacts with conspecifics, hence lower levels of agonistic behaviour should result, as has been reported in other salmonids (see Cole & Noakes

1980). Although the latter tendency was evident in our results, it was not statistically significant.

The amount of food available as invertebrate drift to a territory holder varies directly with current velocity (Everest & Chapman 1972, Wankowski & Thorpe 1979). However, the accompanying increase in hydrodynamic drag, which is roughly proportional to the square of the water velocity (Webb 1975), would more than offset any increase in energy intake this might produce. Therefore, net energy return to a resident would likely decrease if it attempted to defend the same size territory in the same manner as current velocity increased. The responses of the fish in our study to this situation were the same as those when fish density was increased.

First, LD became relatively more frequent and CHS less frequent with increasing current velocity. This same tendency has also been reported in Atlantic salmon (Gibson 1978), coho salmon, *Oncorhynchus kisutch* (Mason 1969) and rainbow trout (Cole & Noakes 1980). However, Mason & Chapman (1965) observed that coho salmon showed more LD and fewer NP in pool areas than in riffle areas of an artificial stream. Similarly, Hartman (1963) reported that brown trout showed fewer LD, relative to NP, with increasing water current velocity. The fact that in the two later cases LD was compared to NP, rather than CHS, may account for the apparent difference in effect of water current on agonistic displays.

Second, territory size decreased with increasing current velocity. This relationship was only apparent though when mean interaction distances were analyzed and not the total area encompassed by the points of interaction. This suggests that although residents responded to an intruder at the same maximum distance regardless of current velocity, they did so less frequently at higher velocities. Kalleberg (1958) reported that as current velocity increased, the number of juvenile Atlantic salmon occupying territories in a stream channel increased. Similarly, interaction distances between juvenile rainbow trout were similar in aquaria with higher water turbulence (Cole & Noakes 1980).

Several hypotheses have recently been proposed to predict how the size of feeding territories should change in response to changes in food abundance. Dill (1978a) and Hixon (1980) predicted that territory size should decrease with increasing food abundance, while Verner (1977) predicted that it should increase (but Verner's hypothesis has been generally criticized, see Krebs & Davies 1981). Ebersole's (1980) model predicts that either result can occur, depending on the territorial strategy of the individual.

Our observation that juvenile brook charr tended (if anything) to increase territory size in response to increased food ration agrees with the prediction from Ebersole's (1980) model. He assumed that feeding territory holders are food energy maximizers (Schoener 1971), striving to maximize fitness as a function of food availability (food density and territory size) minus territorial defense costs (defense time, probability of injury in agonistic encounters, probability of predation). If defense costs are area related and competitor density remains constant, an increase in food abundance should result in an increase in territory size.

Juvenile brook charr (and possibly all territorial young salmonids) appear to be food energy maximizers. Small fish (~ 1g) may have a daily voluntary food intake in excess of 15% live weight, with corresponding high growth rate (Brett 1971). Nutritional insufficiency has been suggested as one of the most important factors related to first year mortality of young salmonids (Gardiner & Geddes 1980). Territorial defense in juvenile brook charr is usually from a single station (or very nearly so), thus defense costs are area-related. Growth rates are directly related to food intake, so fish would obviously benefit if they could maximize net energy intake.

We can undertake at least a preliminary quantitative assessment of the predictions of these opposing hypotheses of changes in territory size with changing food supply from our data. There is a linear relationship between metabolic rate (as inferred from oxygen consumption) and body weight in young salmonids, of the form

$$\log Y = \log a + b \log X, \tag{1}$$

where Y is metabolic rate and X is body weight (Brett 1965). For brook charr, $b = 1.05$ (Beamish 1964). This relationship allows us to quantitatively

test predictions from Ebersole's (1980) model.

If these charr are food maximizers, there should be no significant correlation between body size of individuals and their territory sizes. But if they are feeding time maximizers (Schoener 1971), i.e. maintain a territory only large enough to secure sufficient food for maintenance and some growth, there should be a significant positive correlation between individual body weight and territory size. Our data (Table 6) show no significant correlation ($r = 0.28$, $p > 0.05$, Steel & Torrie 1960). Thus we can conclude that these charr are food maximizers, and so they should increase territory size with increasing food availability (Ebersole 1980). As already discussed, that trend was present in our results.

However, since our data were from a laboratory situation, with physical constraints on the fish (confined within enclosures), contiguous territories and territories not strictly measured as feeding territories, we would hesitate to completely rule out the alternative possibility. Obviously such measurements should be made under field conditions. But basic principles also suggest that these fish should be food energy maximizers, and that they should be able to benefit from (virtually) as much food as they could acquire (Brett & Shelbourne 1975).

Nonetheless, some other findings have been reported that appear to support the alternate viewpoint. McFadden (1969) believed that territory size should vary inversely with food abundance, thereby maintaining a fixed level of food intake (Feeding time minimizers, Schoener 1971). Indeed, Slaney & Northcote's (1974) report that territory size of juvenile rainbow trout was smallest at high food abundance and largest at low food abundance appears to support this view. However, in their study immigration into the feeding area was not controlled and was greatest in the area of highest food abundance. Therefore, changing fish density may have confounded their results and overridden any tendency for fish to expand their territories in response to increasing food abundance. In fact, when they kept fish density constant, territory size did not change in response to changing food abundance (Slaney & Northcote 1974). Symons (1971) and Dill (1978b) likewise found no change in territory size with changing food abundance in either Atlantic salmon or coho salmon, respectively. We conclude from this that there is little, if any, evidence to support the prediction of an inverse relationship between territory size and food abundance.

Ration level may be related to territorial aggression in an ultimate sense, but as yet we do not know over what time period the fish are judging food availability (Dill et al. 1981). Obviously, the response of the fish to different ration levels and changes in ration level would be expected to differ, depending on that time base. Until we have a better measure of that, preferably under field conditions, our conclusions in this regard must remain tentative and conjectural.

Table 6. Body size (length and weight) and territory sizes of individual juvenile brook charr (adopted from McNicol & Noakes 1981).

Fish number	Total length (mm)	Live weight (g)	Territory size (cm^2)
18	41	1.77	1804
5	56	1.20	2029
12	55	1.17	468
10	54	1.04	476
14	43	0.97	887
8	52	1.02	830
17	51	0.87	717
19	49	0.78	1575

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