



## ARTICLES

An experimental analysis of territory size in  
juvenile steelhead trout

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*(Received 30 July 1999; initial acceptance 13 August 1999;  
final acceptance 15 September 1999; MS. number: A8372R)*

I experimentally manipulated levels of food abundance and density of competitors to determine how these factors influence the territory size of juvenile steelhead trout, *Oncorhynchus mykiss*. Steelhead trout were held in artificial stream channels and I followed cohorts that were fed at one of three levels of food abundance and stocked at one of three levels of fish density. By measuring territory size over a 2-month period, while the fish were growing, I was also able to assess the effects of body size in determining the size of a territory. Defended and foraging areas were similar in absolute size, but the frequency of space use was different for defence than for foraging. As predicted, territory size decreased with increasing levels of food abundance and increased with decreasing levels of fish density. In addition, territory size increased with increasing body size even after controlling the effects of food abundance and competitor density. In comparison to previous studies, territory size of steelhead trout changed more dramatically in response to changing levels of food and competitors. For territorial animals with indeterminate growth, territory size is not only adjusted as a trade-off between the costs and benefits of defence, but also with respect to body size due to increasing metabolic demands as individuals grow.

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Territorial behaviour is often viewed as a tactic by which individuals may increase their fitness through the defence and acquisition of resources such as food, shelter, or mates (Brown 1964; Schoener 1971; Davies & Houston 1984). However, because the costs of defence can outweigh the benefits of holding a territory, animals are predicted to defend territories only when there is a net benefit (Brown 1964). Given that an individual has decided to defend a territory, a fundamental question is how large an area should be defended. Territory size is often inversely related to food abundance (Howard 1920; Slaney & Northcote 1974; Stamps 1994) or intruder pressure (Myers et al. 1979; Norton et al. 1982; Eberhard & Ewald 1994). Theoretical models explain these relationships as a trade-off between the costs and benefits of defence, producing an optimal territory area (Schoener 1971; Dill 1978; Ebersole 1980; Hixon 1980).

In addition to the energetic benefits or costs of defence, space requirements for animals are also linked to body size through metabolic demands. Home range or territory

area is known to increase with body size, both inter-specifically (McNab 1963; Schoener 1968; Harestad & Bunnell 1979) and intraspecifically (Stimson 1973; Hart 1985; Elliott 1990; Wada 1993). Hence, for animals that grow substantially while defending a territory, space requirements may also depend on relative body size.

Although past studies provide an indication of the functional relationships between food and competitor abundance and territory size (Myers et al. 1979; Hixon 1980; Schoener 1983; Stamps 1994), most models of optimal feeding-territory size are not appropriate for a mosaic of adjoining territories, also known as contiguous territories (e.g. Barlow 1974; Clayton 1987; Adams 1998). Models for noncontiguous territories assume that individuals are free to adjust their territories without constraint from neighbouring territory boundaries (Grant 1997; Adams 1998). The only model for a contiguous territory size is by Hixon (1980), which predicts a decrease in territory size with food and competitor abundance. Although this same prediction is made for noncontiguous territory size models (Schoener 1983), only Hixon's (1980) model predicts a decrease in territory size with increasing food abundance, if food abundance is sufficiently high. By defending an area within a mosaic of

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contiguous territories, an individual may have its territory compressed beyond the noncontiguous optimum because of the pressure exerted by adjacent neighbours (Hixon 1980). Therefore, territory size will only decrease when food is sufficiently high as to reduce territory size beyond that of the compressed, noncontiguous optimum (Hixon 1980).

Two experimental field studies have attempted to examine the independent effects of food and competitor abundance on the size of contiguous territories in reef fishes. Norman & Jones (1984) studied the effect of food and competitor abundance on the territory size of a pomacentrid reef fish, *Parma victoriae*, and found that density of neighbouring fish and not food abundance influenced territory size. Tricas (1989) found that the territory size of the butterflyfish, *Chaetodon multicinctus*, was primarily influenced by intruder pressure and was only significantly related to food abundance when combined with an increase in intruder pressure. Similarly, when birds occupy contiguous territories, food abundance seems to have little effect on territory size (Franzblau & Collins 1980; Askenmo et al. 1994). These observations are consistent with the idea that food abundance was below that required to reduce territory size beyond the compressed optimum. Given the few and somewhat equivocal results of the above studies, I chose to examine experimentally the influence of food and competitor abundance on the size of contiguous territories of juvenile steelhead trout, *Oncorhynchus mykiss*. Steelhead trout, a stream-dwelling, salmonid fish, is an excellent species to examine this question because salmonids are known to defend feeding territories and adjust their aggressive behaviour to changing environmental conditions (Kalleberg 1958; Cole & Noakes 1980; Dill et al. 1981; McNicol & Noakes 1984). In addition, stream-dwelling salmonids defend feeding territories over a range of body sizes, as they grow (Grant et al. 1989; Elliott 1990; Keeley & Grant 1995; Keeley & McPhail 1998) and so I could examine the influence of territory allometry in conjunction to changing costs and benefits of defence. Specifically, I tested the predictions that territory size is inversely related to food abundance and competitor density for a contiguous territory holder (Hixon 1980). I used a factorial experiment that allowed a comparison of territory sizes under conditions of food abundance and competitor density that varied by 400%, and I followed the change in territory size as fish grew, allowing me to assess whether all three factors have significant independent effects on territory size.

## METHODS

### Collection and Rearing of Animals

On 5 May 1995 I collected eight male and two female adult steelhead trout, from the Chilliwack River, British Columbia (49°4.8'N, 122°42.8'W) to use as broodstock. To maximize the genetic variability from my sample of the parent population, I divided the eggs from a single female into eight equal parts and fertilized each part with the sperm from one of eight males. Hence, I used 16 crosses,

based on the eggs of two females and the sperm of eight males, as the source of juvenile trout. I incubated the embryos in a single upwelling incubation bottle, supplied by 8°C groundwater at the Fraser Valley Trout Hatchery (49°0.9'N, 122°16.4'W), near Abbotsford, British Columbia. When the embryos reached the eyed stage of development, I moved them to the Cultus Lake Laboratory (49°3.3'N, 122°1.4'W) and placed them in metal baskets suspended in a fibreglass trough that was supplied with 10°C water drawn from Cultus Lake, British Columbia (49°3.3'N, 122°1.0'W). All fish were kept in the trough until they had absorbed their yolk sac and had begun to feed exogenously.

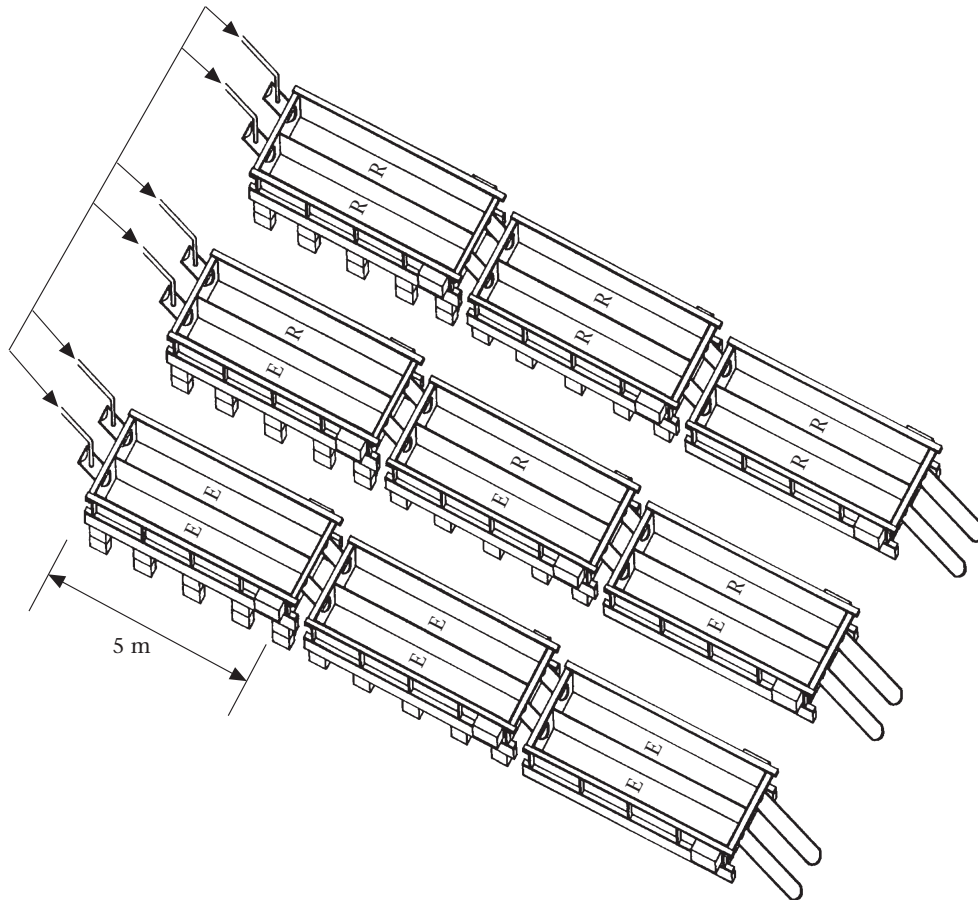
### Experimental Set-up

I constructed 18 artificial stream channels on the outdoor compound at the Cultus Lake Laboratory. Each channel measured 5 × 0.92 m wide and 0.40 m deep. Channels were constructed from plywood sheets supported by '2 × 4' match lumber and lined with polyurethane tarpaulins, then sealed with silicone to make them watertight. To conserve the large volume of water required to simulate flow from a natural stream, I arranged the 18 channels in a blocked, staircase design (Fig. 1) with channels grouped into columns of three. Water was introduced to an upper channel, which then flowed into the next highest channel, and then to a third channel that was placed level with the ground, directly behind the second channel (Fig. 1; also see Keeley 1998). I constructed six such columns of three channels for a total of 18 individual experimental units. The downstream end of each connecting trough was screened to prevent the escape of any fish.

To simulate flow over a natural substrate, I placed a single layer of stream gravel, (particle range 5–10 cm in diameter) into each of the channels. To guard against aerial predators, I placed a canopy of burlap material above the top edge of each channel. The burlap also acted as a blind for observers and equalized the shade over channels, while still permitting enough light to pass through to the water, allowing fish to feed and interact with each other.

As part of a companion study designed to estimate numbers of fish being excluded from foraging in the channel due to competition, each channel had a Plexiglas box (62 × 29.5 cm and 26 cm high) attached to the side and downstream end (Fig. 1). The results from this part of the experiment are reported elsewhere (Keeley 1998).

Water was supplied to the channels from a 1700-litre tank that was filled from two large reservoirs supplied by water drawn above and below the thermocline, from nearby Cultus Lake. By mixing water from above and below the lake thermocline, I maintained the experimental water temperature at an average ± SD of 13.3 ± 1.1°C. Each channel received 435 litres of water per minute from the 1700-litre tank, producing a flow that averaged 7 cm/s and 10 cm deep. I filtered water entering the tank using fine-mesh nylon screening to remove any invertebrates that might have entered from the lake water. In addition, I also placed small nets constructed from the same



**Figure 1.** The design and layout of stream channels (E: experimental; R: replicate) used in the experiment. Arrows indicate input and direction of water flow to the top of the uppermost channels.

material in the troughs connecting each channel to prevent any excess food from drifting between experimental units.

Over a 2-month period, I tested the effects of food and competitor density on the behaviour of juvenile trout in the experimental set-up described above. All fish were sampled from the original stocking pool over a 6-h period on 31 July 1995 and removed over an 8-h period on 25 September 1995. To manipulate levels of food abundance and competitor density, I stocked the stream channels at one of three levels of fish density and introduced food at one of three levels of food abundance. I chose densities of fish to represent the range of densities observed in wild populations (Elliott 1994) and to test whether minimum space requirements limit the density of salmonids in streams (Grant & Kramer 1990; Keeley 1998).

When stocking fish into an experimental unit, I captured 10–20 individuals from the pool of fish that I had reared from embryos, and randomly assigned them to one of 18 holding containers. I repeated this procedure until I had enough individuals in each container to represent one of the three densities of fish. A channel received either 582, 291 or 146 fish (mean  $\pm$  SD fork length =  $3.18 \pm 0.13$  cm) and a daily ration of dry extruded pelleted food (15% size grade 1, Biodiet<sup>®</sup>, 85% size grade 2, Biodry<sup>®</sup>; Bioproducts, Warrenton, Oregon). The high,

intermediate and low levels of food ration were 5.76, 2.88 and 1.44 g/day, respectively. Because stream salmonids feed primarily on invertebrate drift (McNicol et al. 1985; Wilzbach et al. 1986; Keeley & Grant 1995), I fed fish such that artificial food items would be presented in a manner similar to that of encountering invertebrate drift. I chose the size grade of pelleted food to simulate the average size of invertebrates encountered by stream salmonids (Keeley & Grant 1997). To simulate the low constant rate of daytime invertebrate drift (Waters 1972; Rader 1997), I introduced the daily ration of food over a 12-h period, using an automated belt feeder attached to the top of each channel. Beginning at 0700 hours each day, I spread the ration of food evenly over a flat belt 20 cm wide by 50 cm long, contained in an open-bottom, rectangular, plastic box. A slowly turning gear, set on a 12-h clock controlled each belt. As the gear turned, the belt would move, tipping a small portion of the food into the channel current at a constant rate.

I assigned treatment levels using the array of channels as a blocking factor (cf. Neter et al. 1990) to remove any potential upstream–downstream effects of treatment position. For nine of the channels (the first three columns of three channels; Fig. 1), I assigned experimental treatments such that each level of the experimental factors appeared once in the upper, middle and lower channel

positions. Hence, any pattern observed from the experimental treatments could not be attributed to a consistent position in the experiment because each occupied a different position across the array of channels. I repeated this procedure for a second set of nine channels to provide a second replicate for all treatment levels. I checked and observed each channel regularly to ensure water continued to flow equally in all channels. Daily maintenance of the stream channels consisted of cleaning small debris from downstream screens, as well as the nets filtering the water between channels, every 12 h.

### Behavioural Measurements

To measure the behaviour of fish in a stream channel, I videotaped a metre-long section of each channel for 30 min every 2 weeks, using an S-VHS video camera on a tripod, angled through an opening in the burlap canopy. Between consecutive taping dates, I randomized the order of videotaping, so that each channel was not observed at the same time of day over the course of the experiment. From each 30-min segment of videotape, I recorded the behaviour from a random sample of five fish (hereafter the focal fish) foraging from a centrally located station over the channel bottom. I did not use the first 5 min of each 30-min segment because sometimes I disturbed the fish while setting up the camera and the 5-min period allowed fish time to return to their foraging positions. Although I did not always measure the territory size of fish in adjoining territories, I assumed that fish were defending contiguous territories because fish in the videotaped area always appeared to be surrounded by other individuals maintaining a foraging station. When calculating a behavioural response from a stream channel, I used the mean of the five focal fish to represent the behavioural response from an experimental population. Hence, I considered the stream channel to be the unit of replication in this experiment and not the number of individuals observed in a stream channel.

To collect data from videotapes, I projected video images on pieces of Mylar sheeting and marked the foraging and aggressive distances of focal fish. I considered foraging distances to be the distance travelled by a fish from its holding station to the point where it intercepted a potential food item. Although fish did not always appear to eat a potential food item, I measured the first 10 attempts for each of the five fish for each taping bout. I considered aggressive distance to be the distance travelled by a focal fish from its holding station to the point where an intruding fish elicited an aggressive response. Although salmonids have been observed to use several types of aggressive behaviour when defending a territory (Brown & Brown 1993), I chose to use chases and lateral displays because they could be reliably measured from the video images. Previous studies of salmonids in natural streams have found that there is no difference in territory size when described by a range of aggressive behaviour patterns (Keeley & Grant 1995; Keeley & McPhail 1998). Hence, I compiled all behavioural distances to calculate territory radius (see below). To calculate actual distances from the video images, I rescaled the

image by using a correction factor created from a system of grid lines, spaced 10 cm apart, that were drawn on the walls of the channels and on a thin rope placed down the bottom centre of each channel. I then used a BASIC programmed digitizing tablet that calculated distance based on the correction factor. Using these digitized behavioural distances as an average radius, I calculated territory size as the area of a circle (Keeley & Grant 1995; Keeley & McPhail 1998). I also measured body size of fish in the channel using this same system.

Upon completion of the experiment, subject animals were killed with an overdose of anaesthetic as required by the collecting and rearing permit issued by the British Columbia Ministry of Fisheries.

### Ethical Note

The British Columbia Ministry of Fisheries' requirement to dispose of experimental subjects arises from the concern that diseases might be transmitted from hatcheries to wild populations. Because of the variety of pathogens and the length of incubation for some diseases, it is not logistically possible for Government biologists to test research studies for disease. Hence, they insist that experimental subjects be destroyed rather than released into wild populations.

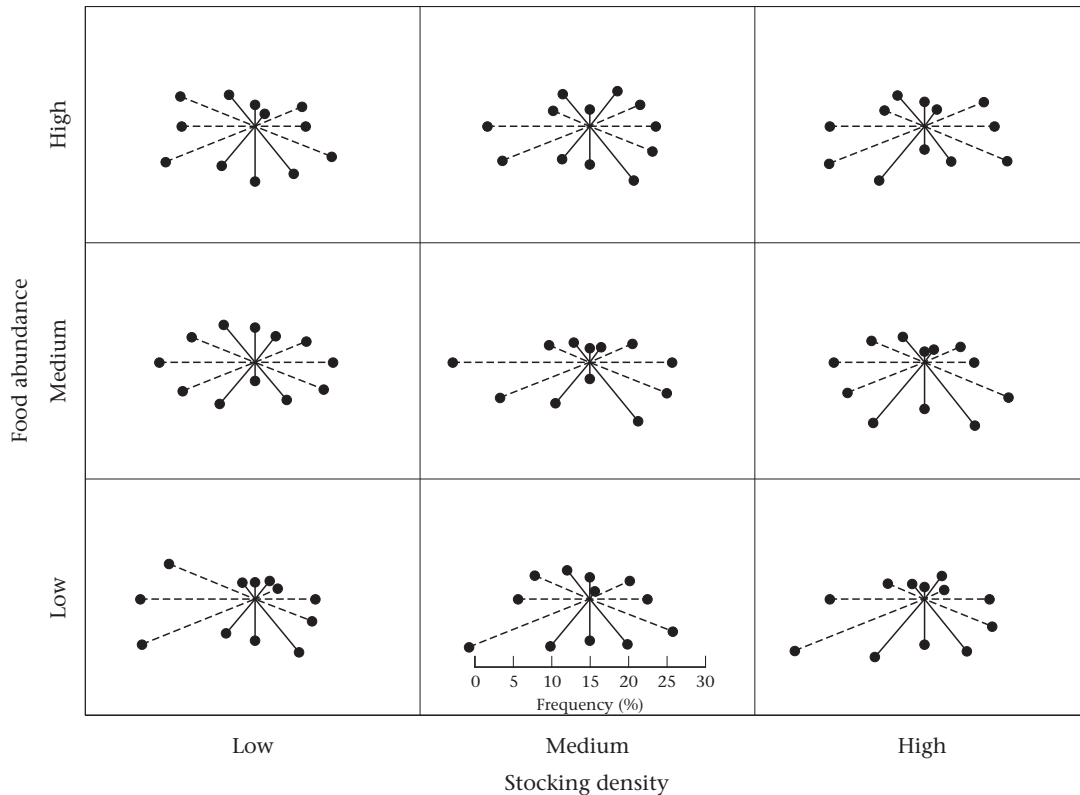
### Statistical Analyses

Because I had made repeated observations over the course of the experiment, I used a two-factor repeated measures analysis of variance (ANOVA) to assess the effects of food abundance and stocking density on the behaviour of the steelhead trout held in the stream channels. When the assumption of sphericity of the variance-covariance matrix for a repeated measures analysis of variance was not met, I applied a Huynh-Feldt correction of *P* values (SAS Institute 1989). When repeated measurements were not made, I used a univariate two-factor analysis of variance (ANOVA) to assess treatment effects. To ensure that all least-squares tests met the assumption of normality of error variance, I checked the residuals from all ANOVA and regression models. When required, I log transformed response variables to meet this assumption. All analysis of variance tests of significance are based on type-III sum of squares (SAS Institute 1989) and are two tailed.

## RESULTS

### Foraging Behaviour

Juvenile steelhead trout captured food items in all directions surrounding a centrally located foraging station; however, the distribution of effort was not equal (Fig. 2). Overall, 60.6% of foraging attempts were directed towards lateral directions of the foraging area, and 27.2 and 12.6% were directed towards the down and upstream directions, respectively. Although the distribution of foraging effort was not identical in all treatment levels (Fig.



**Figure 2.** The relative frequency of foraging attempts made in 12 directions from a holding station by juvenile steelhead trout, according to nine experimental treatment combinations. The direction of current in the stream channels is from the top to the bottom of the figure. ---: Foraging attempts in lateral directions; —: foraging attempts in upstream and downstream directions.

2), the general pattern was consistent between treatments (Kendall's coefficient of concordance:  $w=0.84$ ,  $N=18$ ,  $P<0.001$ ). The frequency of foraging was highest in lateral directions in comparison to the upstream and downstream directions. To assess the shape of the foraging area, I paired comparisons by experimental stream channel and I considered  $P$  values to be significant if  $P\leq 0.008$  (Bonferroni correction; Neter et al. 1990). Foraging areas were bilaterally symmetrical; the frequency of foraging attempts did not differ between the left and right quadrants of the foraging area (paired  $t$  test:  $t_{17}=1.89$ ,  $P=0.076$ ; Fig. 2). In addition, the frequency of foraging attempts downstream did not differ from the average frequency in the lateral quadrants (paired  $t$  test:  $t_{17}=1.78$ ,  $P=0.093$ ; Fig. 2), but there were more foraging attempts downstream than upstream (paired  $t$  test:  $t_{17}=13.51$ ,  $P<0.0001$ ; Fig. 2) and fewer attempts upstream compared with the average frequency in the lateral quadrants (paired  $t$  test:  $t_{17}=17.10$ ,  $P<0.0001$ ; Fig. 2). Fish tended to move laterally most often, but moved only infrequently upstream to capture food (Fig. 2).

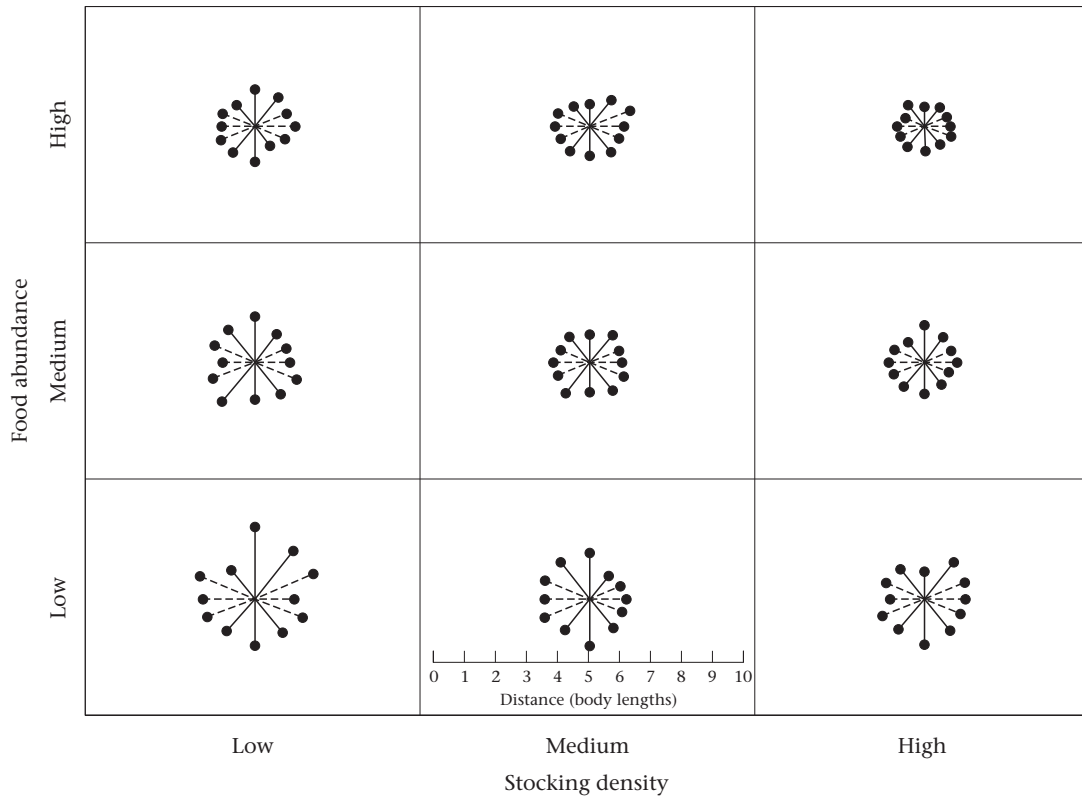
Despite the difference in orientation of foraging effort, the distance travelled (in body lengths) by fish was similar in all directions (Fig. 3). There was no significant difference in foraging distances between the upstream and downstream quadrants (paired  $t$  test:  $t_{17}=0.014$ ,  $P=0.99$ ; Fig. 3) or between the left and right quadrants (paired  $t$  test:  $t_{17}=1.24$ ,  $P=0.23$ ; Fig. 3). The average distance travelled in the lateral quadrants was about 11

and 12% smaller than the upstream (paired  $t$  test:  $t_{17}=4.38$ ,  $P=0.0004$ ; Fig. 3) and downstream directions (paired  $t$  test:  $t_{17}=6.45$ ,  $P<0.0001$ ; Fig. 3), respectively. Mean foraging distance was related to both food abundance and stocking density (Fig. 4). Foraging distance decreased with increasing food abundance (ANOVA:  $F_{2,9}=35.79$ ,  $P<0.0001$ ; Fig. 4) and decreased with increasing stocking density (ANOVA:  $F_{2,9}=14.62$ ,  $P=0.0015$ ; Fig. 4). In addition, the variance in foraging distance increased with decreasing food abundance (ANOVA:  $F_{2,9}=6.30$ ,  $P=0.02$ ; Fig. 4) and decreased with increasing stocking density (ANOVA:  $F_{2,9}=4.79$ ,  $P=0.038$ ; Fig. 4).

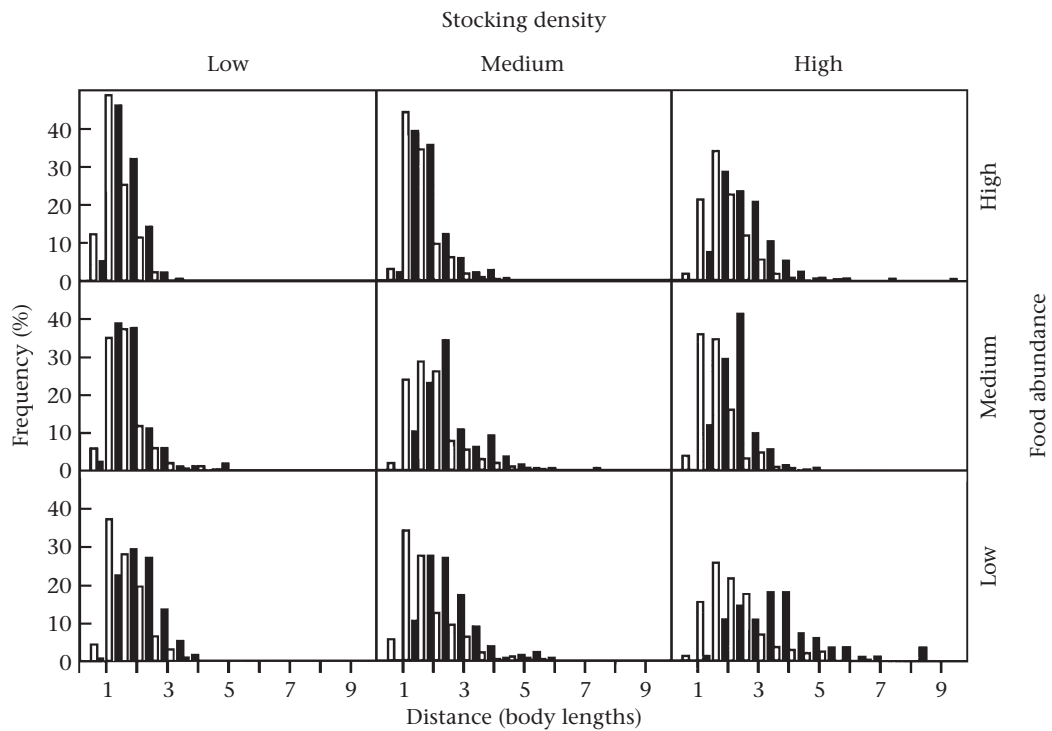
Average foraging rates varied considerably during the experiment from 2.90 to 7.82/min (mean 5.21/min). Foraging rate was not related to food density (ANOVA:  $F_{2,8}=2.52$ ,  $P=0.14$ ; Fig. 5a–c) or stocking density (ANOVA:  $F_{2,8}=0.14$ ,  $P=0.87$ ; Fig. 5a–c), over the course of the experiment, but foraging rates did increase significantly between weeks 4 and 8, when averaged over all treatment levels (ANOVA:  $F_{2,24}=8.87$ ,  $P=0.0004$ ; Fig. 5a–c).

### Aggressive Behaviour

Juvenile steelhead trout defended the areas in which they foraged, but the distribution of effort was not equal in all directions (Fig. 6). Despite the difference in aggressive effort between upstream, downstream and lateral directions, the general pattern of aggressive effort was consistent among treatment levels (Kendall's coefficient



**Figure 3.** The average distance in body lengths of foraging attempts made by juvenile steelhead trout in 12 directions. All other details as in Fig. 2.



**Figure 4.** Frequency distribution of foraging attempts (□) and aggressive acts (■) in relation to the distance from the centre of a foraging station for nine experimental treatment combinations.

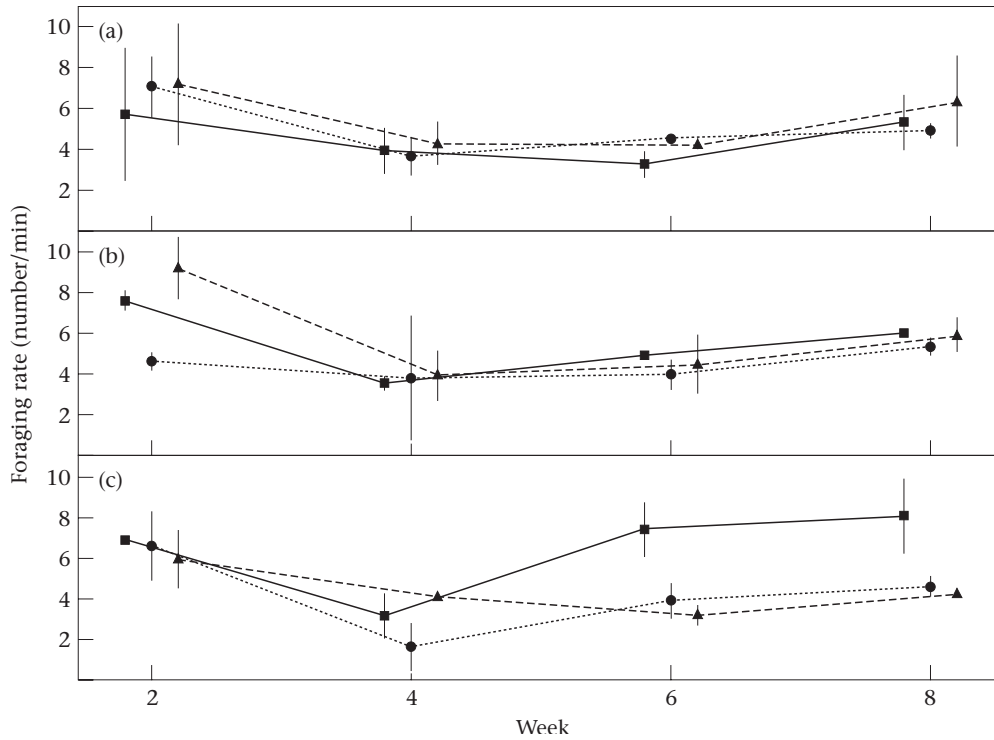


Figure 5. Foraging rates of juvenile steelhead trout under (a) high, (b) medium or (c) low stocking densities at 2-week intervals. Symbols depict mean±SE for high (■), medium (●) or low (▲) levels of food abundance.

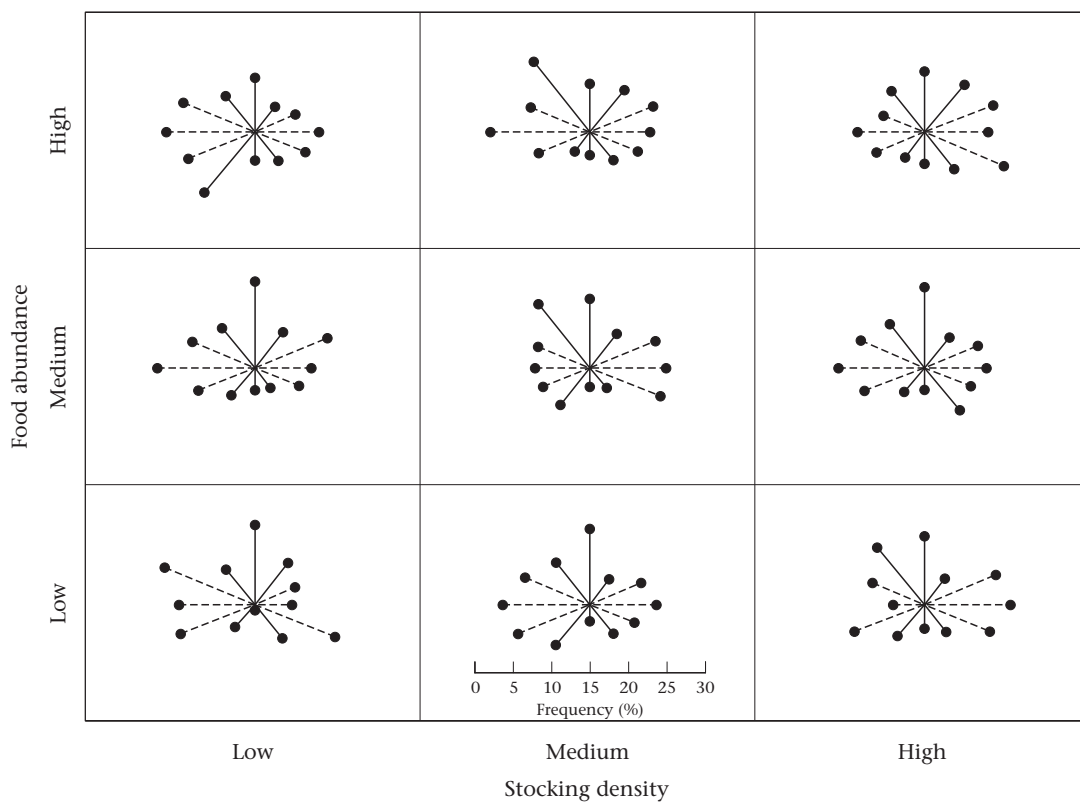
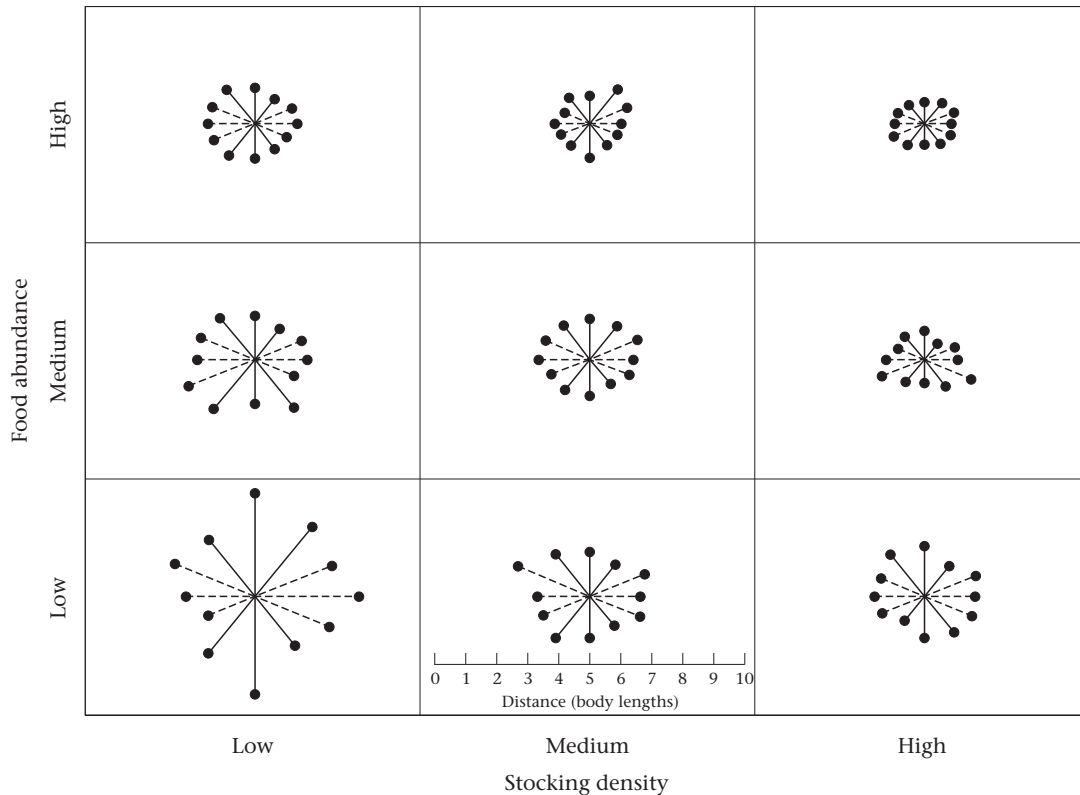


Figure 6. The relative frequency of aggressive acts made in 12 directions from a holding station by juvenile steelhead trout, according to nine experimental treatment combinations. All other details as in Fig. 2.



**Figure 7.** The average distance (in body lengths) of aggressive acts made by juvenile steelhead trout in 12 directions, according to nine experimental treatment combinations. All other details as in Fig. 2.

of concordance:  $w=0.64$ ,  $N=18$ ,  $P=0.001$ ; Fig. 6). To assess the shape of the defended area, I paired comparisons by experimental stream channel and I considered  $P$  values to be significant if  $P \leq 0.008$  (Bonferroni correction; Neter et al. 1990). Defended areas were bilaterally symmetrical because there was no difference in the frequency of defence effort between left and right quadrants (paired  $t$  test:  $t_{17}=0.95$ ,  $P=0.36$ ; Fig. 6) or in comparison to the average of the two lateral quadrants versus the upstream direction (paired  $t$  test:  $t_{17}=1.36$ ,  $P=0.19$ ; Fig. 6). Significantly less effort was directed downstream compared with upstream (paired  $t$  test:  $t_{17}=5.17$ ,  $P<0.0001$ ; Fig. 6), or the average of the lateral quadrants (paired  $t$  test:  $t_{17}=6.63$ ,  $P<0.0001$ ; Fig. 6). On average, aggressive behaviour was directed towards the upstream quadrant 29.6% of the time, followed by the left (27.2%) and right (26.0%) lateral quadrants, and least often downstream (17.1%).

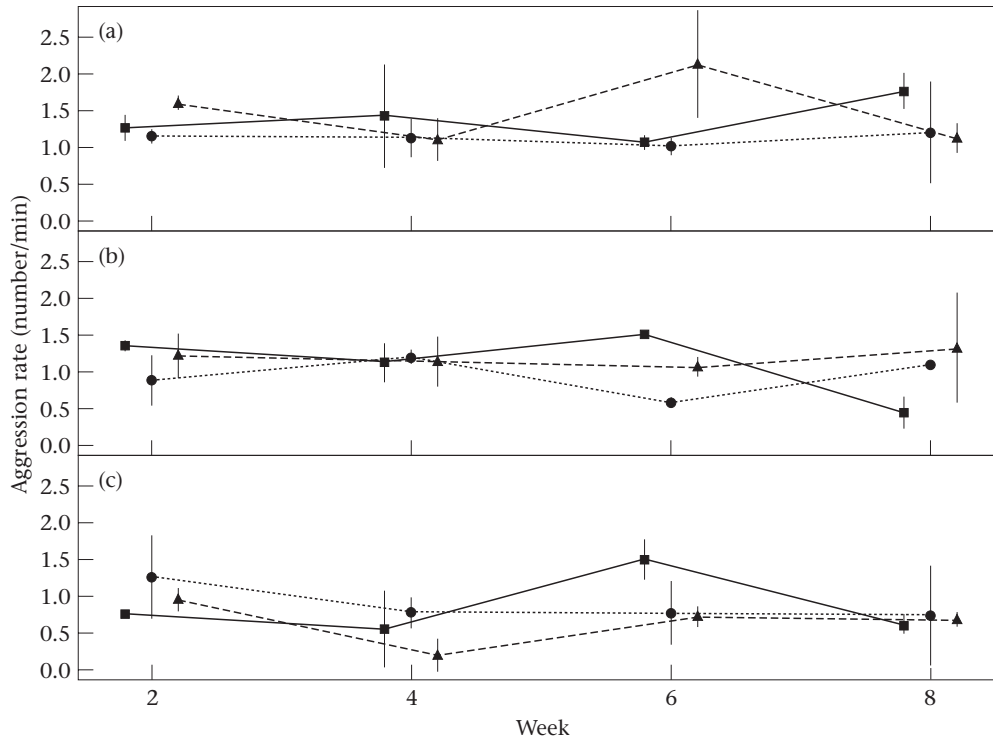
Although most defence effort was primarily directed laterally and upstream of the holding station, the shape of the defended area was roughly circular (Fig. 7). There was no difference in aggressive distance between left or right quadrants (paired  $t$  test:  $t_{17}=0.52$ ,  $P=0.61$ ; Fig. 7), upstream versus downstream (paired  $t$  test:  $t_{17}=1.46$ ,  $P=0.16$ ; Fig. 7), or between the average of the lateral quadrants and downstream (paired  $t$  test:  $t_{17}=1.38$ ,  $P=0.19$ ; Fig. 7) or upstream (paired  $t$  test:  $t_{17}=2.71$ ,  $P=0.015$ ; Fig. 7). In contrast, the mean aggressive distance was related to experimental treatment levels (Fig. 7). Mean aggressive distance decreased with increasing food

abundance (ANOVA:  $F_{2,9}=39.39$ ,  $P<0.0001$ ; Fig. 4) and increased with decreasing stocking density (ANOVA:  $F_{2,9}=23.02$ ,  $P=0.0003$ ; Fig. 4). In addition, the variance in aggressive distance increased with decreasing food abundance (ANOVA:  $F_{2,9}=26.96$ ,  $P=0.0002$ ; Fig. 4) and decreased with increasing stocking density (ANOVA:  $F_{2,9}=14.81$ ,  $P=0.0014$ ; Fig. 4).

Aggressive interactions were much less frequent than foraging attempts. When averaged over all experimental conditions, aggressive rates averaged 1.22/min and had an average minimum and maximum of 0.57 and 2.0/min, respectively. Rates of aggression were not related to the abundance of food in experimental stream channels (ANOVA:  $F_{2,8}=0.73$ ,  $P=0.51$ ; Fig. 8) and there was no consistent increase or decrease in aggression rates over the course of the experiment (ANOVA:  $F_{3,24}=0.81$ ,  $P=0.50$ ; Fig. 8); however, when integrated over the 8-week period, rates of aggression increased with increasing stocking density (ANOVA:  $F_{2,8}=12.67$ ,  $P=0.0033$ ; Fig. 8).

### Comparison of Defended and Foraging Areas

Juvenile steelhead trout foraged and defended space around a primary holding station, but the relative use of space for defence and foraging was different (Figs 2, 3 versus Figs 5, 6). While both foraging and aggressive distance were inversely related to food abundance and stocking density (see results above), the rate of change was higher for aggressive than for foraging distance. The



**Figure 8.** Aggression rates of juvenile steelhead trout under (a) high (b) medium or (c) low stocking densities at 2-week intervals. Symbols depict mean  $\pm$  SE for high (■), medium (●) or low (▲) levels of food abundance.

mean difference in body lengths between foraging and aggressive radii was large at the low food level, but decreased with increasing food abundance (ANOVA:  $F_{2,9}=22.55$ ,  $P=0.0003$ ; Fig. 4) and increasing stocking density (ANOVA:  $F_{2,9}=17.77$ ,  $P=0.0007$ ; Fig. 4).

In all treatment levels, mean aggressive radius was larger than mean foraging radius (paired  $t$  test:  $t_{17}=4.81$ ,  $P=0.0002$ ). Fish tended to defend space most often at intermediate distances, whereas the frequency of feeding decreased with increasing distance from the holding station (Fig. 4). In contrast, the average maximum foraging and aggressive radii did not differ significantly when paired by experimental treatment level (paired  $t$  test:  $t_{17}=0.87$ ,  $P=0.40$ ; Fig. 4). This suggests that there are relative but not absolute differences in space use for foraging and defence that are both affected by levels of food abundance and competitor density. In fact, foraging distance increased significantly with aggressive distance, even after statistically controlling for the effects of food abundance, stocking density and fish size (partial  $r=0.20$ ,  $N=68$ ,  $P=0.02$ ).

### Effects on Territory Size

The size of defended areas increased significantly over the course of the experiment in all treatments (Fig. 9, Table 1); however, territory size was also dependent on the level of food abundance and stocking density (Fig. 9). At each level of stocking density, territory size was largest in the lowest level of food abundance and decreased significantly with increasing food abundance (Fig. 9, Table 1). Similarly, at each level of food

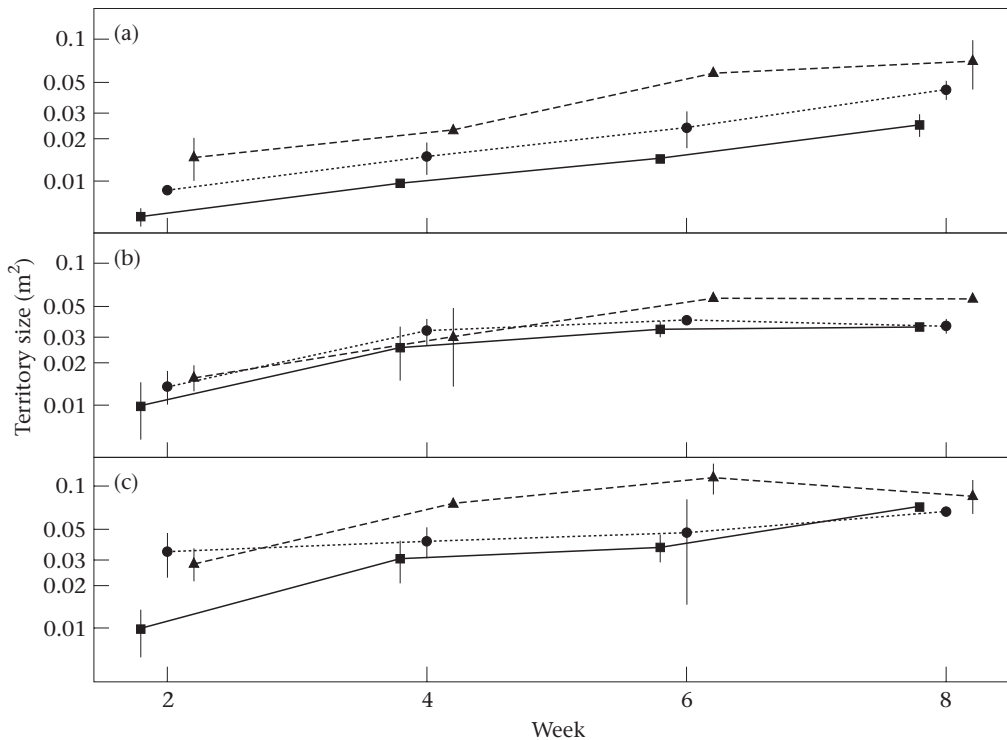
abundance, territory size was largest in the lowest stocking density and decreased significantly with increasing stocking density (Fig. 9, Table 1).

To examine the allometry of territory size, I used a multiple regression approach and compared estimates of territory size and fish body size at each 2-week interval for each stream channel. After statistically controlling for the effects of food abundance and fish stocking density, territory size increased significantly with fish size (Fig. 10). As demonstrated by the repeated measures analysis of variance (Fig. 9; Table 1), food abundance and stocking density were again inversely related to territory size using the multiple regression analysis (Table 2). The multiple regression model that describes territory size is:  $\log \text{territory size (m}^2\text{)} = 3.49 \log \text{fish length (cm)} - 0.17 \text{ food abundance (g/day)} - 0.078 \text{ stocking density (number/m}^2\text{)} - 3.029$ ;  $R^2=0.73$ ,  $N=72$ ,  $P<0.0001$ .

## DISCUSSION

### Foraging versus Aggressive Behaviour

Models of optimal foraging area predict that animals adjust their behaviour in response to changing environmental conditions so as to maximize their energy intake (Stephens & Krebs 1986). Although the fish in this experiment tended to move laterally from their foraging stations in all treatment combinations (Fig. 2), the distance they travelled (in body lengths) decreased with increasing food abundance and competitor density (Fig. 3). As for several models of optimal feeding-territory size (Schoener 1983), both Andersson's (1978) and Schoener's



**Figure 9.** Territory size of juvenile steelhead trout at 2-week intervals, under conditions of (a) high, (b) medium and (c) low stocking densities. Symbols depict mean  $\pm$  SE for high (■), medium (●) or low (▲) levels of food abundance.

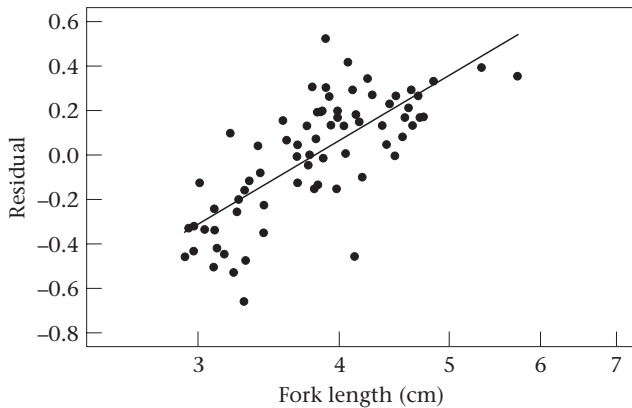
**Table 1.** Repeated measures ANOVA results for experimental treatment effects on territory sizes of steelhead trout at 2-week intervals

Source	MS	df	F	P
Within-subject effects				
Time	1.15	3	36.69	<0.0001
Time $\times$ food abundance	0.035	6	1.12	0.38
Time $\times$ stocking density	0.027	6	0.87	0.53
Time $\times$ stocking density $\times$ food abundance	0.020	12	0.65	0.78
Between-subjects effects				
Food abundance	0.67	2	32.77	<0.0001
Stocking density	0.71	2	30.59	<0.0001
Food abundance $\times$ stocking density	0.040	4	1.85	0.20
Error	0.022	9		

(1979) model of central-place foraging predict a decrease in foraging area with increasing food abundance. However, unlike territory-size models, foraging models also predict a decrease in foraging effort with distance from the central place because travel costs increase with distance from the prey. Steelhead trout in my experiment tended to forage most often closer to the central holding station in all treatments, but the variance in foraging distance increased as food abundance increased or competitor pressure decreased (Fig. 4). Unlike foraging effort, the distribution of aggressive behaviour was most often directed upstream of a holding station, but was again consistent among treatment levels (Fig. 6). The fish in this experiment defended upstream directions most often, presumably to prevent competitors from consuming food that was drifting onto their territories, as steelhead trout and other salmonids do in natural streams

(Grant et al. 1989; Keeley & Grant 1995; Keeley & McPhail 1998). Average aggressive radius decreased with increasing food and competitor abundance (Fig. 7), but was larger than the mean foraging radius in all treatments and tended to be much more frequent at intermediate distances in comparison to foraging effort (Fig. 4). In contrast, maximum aggressive and foraging radii did not differ significantly. Therefore, while there were relative differences in the direction and frequency of space use, when the absolute use of space is considered, foraging and defended areas were equal in size, as assumed by models of optimal feeding-territory size (Schoener 1983).

Defended and foraging areas are not always equal in size. For animals that defend territories for reproduction as well as feeding, such as coral reef fishes (Myrberg & Thresher 1974; Thresher 1976), the area used for foraging is the same as the area defended against heterospecifics



**Figure 10.** Residual variation from a territory size versus food and competitor abundance regression in relation to fish length. Equation of the line is:  $\text{residual} = 3.053 \log \text{fork length (cm)} - 1.77$ ,  $r^2 = 0.55$ ,  $N = 68$ ,  $P < 0.0001$ .

**Table 2.** Multiple regression statistics for several variables predicting territory size in juvenile steelhead trout

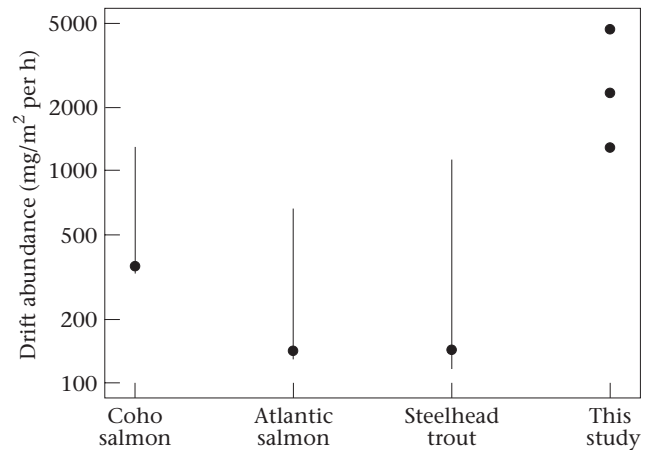
Variable	Coefficient	SS*	P*
Food abundance	-0.17	0.63	<0.0001
Stocking density	-0.078	0.15	0.034
Food abundance × stocking density	0.0023	0.00089	0.87
Fish length (cm)	3.49	3.27	<0.0001

\*Sum of squares and the probability for each variable, when entered into the model after all other variables.

with similar dietary requirements, but is larger than that defended against nest predators. In my study, the sizes of defended and foraging areas were the same, perhaps because they served only to capture food.

### Factors Influencing Territory Size

Models of optimal feeding-territory size often make different predictions for the effects of food and competitor abundance, depending on the goals of the forager (Schoener 1983; Grant 1997). For energy-maximizing animals, like fish, territory-size models usually predict a decrease in territory size with food and competitor pressure (Schoener 1983; but see Ebersole 1980). For salmonid fish that often occupy contiguous territories in the wild (Grant et al. 1989; Elliott 1990; Keeley & Grant 1995), models of feeding territory size predict either a decrease or no change (Dill 1978) or an increase or decrease in territory size (Grant & Noakes 1987). However, only Hixon (1980) has modelled the response for contiguous territories and he found that food abundance should affect territory size only at sufficiently high levels. This model may therefore explain the findings of observational and experimental studies of territory size in fish that have either failed to detect an effect of food abundance (Symons 1971; Norman & Jones 1984), found only a weak relationship (Dill et al. 1981; Keeley & Grant 1995; Keeley & McPhail 1998) or have found an effect when



**Figure 11.** The abundance of drifting aquatic invertebrates (mean  $\pm$  range) encountered near or over salmonid fish territories for coho salmon (Dill et al. 1981), Atlantic salmon (Keeley & Grant 1995), steelhead trout (Keeley & McPhail 1998), and in comparison to the ration delivered to experimental stream channels (this study).

food abundance was accompanied by an increase in intruder pressure (Slaney & Northcote 1974; Tricas 1989). In my study, where food abundance was manipulated at levels that approximated the upper range of food levels found in streams, as well as levels two and four times this base level (Dill et al. 1981; Keeley & Grant 1995; Keeley & McPhail 1998), the response was much stronger. Food abundance accounted for 46% of the variation in territory size, approximately 9–20 times the amount previously detected for salmonids in the wild (Dill et al. 1981; Keeley & Grant 1995; Keeley & McPhail 1998). I know of only three studies that have quantified the abundance of invertebrate drift over salmonid territories during periods of time when fish are actively foraging in natural streams (Fig. 11). These studies indicate that although drift abundance is variable, the ranges are largely overlapping and tend to be lower than the ration of food I delivered to my stream channels. These data suggest that only very large increases in invertebrate production would decrease territory size in natural streams and would at least partly explain why measures of territory size changed so little in previous studies (Grant et al. 1998).

Most models of territory size predict a decrease in territory size with increasing competitor pressure (Dill 1978; Ebersole 1980; Schoener 1983), including Hixon's (1980) model. Several studies have found an inverse relationship between territory size and competitor abundance in birds (Myers et al. 1979; Norton et al. 1982), reef fish (Norman & Jones 1984; Tricas 1989) and stream-dwelling salmonids over a large range of densities (McNicol & Noakes 1984; Keeley & McPhail 1998) and not at narrower densities (Dill et al. 1981; Keeley & Grant 1995). Using densities that ranged by 400%, I found that territory size was strongly related to competitor density, independently accounting for 42% of the variation in territory size. My study indicates that food and competitor abundance independently influence territory size for a contiguous territory holder. However, in comparison to

previous studies of territory size in reef (Norman & Jones 1984; Tricas 1989) and salmonid fish (Dill et al. 1981; McNicol & Noakes 1984; Keeley & Grant 1995; Keeley & McPhail 1998), the response is much stronger than previously observed.

Although there have been numerous models of optimal-feeding territory size, most models assume that food or competitor abundance are the primary determinants of territory size (Schoener 1983). Empirical studies of salmonid fish have shown that individuals may be less aggressive towards kin than nonkin (Brown & Brown 1993, 1996) and individuals that hold a territory tend to be less likely to be eaten than nonterritorial fish (Symons 1974). Hence, future studies may consider how levels of relatedness and risk of predation influence the size of a defended area, particularly because territory size may act as a limit to population abundance (Grant & Kramer 1990; Newton 1992; Keeley 1998).

### Allometry of Territory Size

Although body size was first proposed as a primary determinant of space requirements in animals 35 years ago (McNab 1963), interspecific allometric studies have usually ignored intraspecific variation in body size (Schoener 1968; Turner et al. 1969; Harestad & Bunnell 1979). This is probably because the range of body sizes of most species used in interspecific allometric regressions is relatively narrow. For territorial species with indeterminate growth, however, the change in body size can be very dramatic. For example, juvenile Atlantic salmon, *Salmo salar*, and steelhead trout begin defending feeding territories at 2–3 cm in length or 0.1–0.15 g, until they migrate to the ocean at about 14–18 cm or between 30 and 65 g (Maher & Larkin 1954; Keenleyside & Yamamoto 1962; Keeley & Grant 1995; Keeley & McPhail 1998). Hence, fish increase in body length by almost an order of magnitude and by over two orders of magnitude in mass. Therefore, increasing metabolic demands predict that even if fish were optimizing the trade-off between the costs and benefits of defence, individuals would have to increase territory size to capture sufficient food. This study is the first experimental study I know of that has provided evidence to support the idea that animals adjust the size of the area they defend not only based on the level of food or competitor abundance, but also based on their own body size.

If animals scale their territory to meet energetic demands, then territory size should scale at the same rate as metabolic rate scales to body mass. In birds, mammals and lizards, territory or home-range size scales faster than expected by metabolic rate (Schoener 1968; Turner et al. 1969; Harestad & Bunnell 1979). On average, metabolic rate scales to body mass by the exponent 0.87 in salmonid fish (Steingrímsson & Grant 1999). In steelhead trout (Keeley & McPhail 1998) and for several other salmonid species (Grant et al. 1989; Elliott 1990; Keeley & Grant 1995), the scaling of territory size is consistent with the metabolic rate hypothesis. In this study, territory size was related to body length according to a slope of 3.49. Because length is related to mass in salmonids by an

exponent of 3.03 (Grant & Kramer 1990), territory size scales to mass by the exponent 0.87, again consistent with metabolic rate. Therefore, unlike terrestrial animals, the data for salmonid fish suggest that territories increase in size to meet increasing metabolic demands.

In summary, juvenile steelhead trout in experimental stream channels defended territories that were influenced in size by both food abundance and the number of competitors. Territory size also increased in size over the course of the experiment, due to increased metabolic demands from growth. Future studies of territorial animals with indeterminate growth should consider both environmental influences of territory size as well as the importance of body size in determining the size of a defended area.

### Acknowledgments

My research was supported by grants from le Fonds pour la Formation de Chercheurs et l'Aide à la Recherche du Québec, the British Columbia (B.C.) Ministry of Environment, Lands and Parks, The Steelhead Society of B.C., and by a Postdoctoral Fellowship from Forest Renewal B.C. Additional funding was provided by NSERC operating grant to J. D. McPhail. I thank K. D. Fausch, J. S. Griffith, G. Iwama, N. R. Liley, J. D. McPhail, J. N. M. Smith, D. Schluter, E. B. Taylor and R. Turkington for helpful comments and discussions on the manuscript. Two anonymous referees also provided helpful comments. The Department of Fisheries and Oceans (Chilliwack River Hatchery and Cultus Lake Laboratory) and the B.C. Ministry of Environment, Lands and Parks (Fraser Valley Trout Hatchery and Fisheries Branch) provided logistical support. I also thank D. Buxton, B. Gordon, K. Morton, K. Scheer, B. Smith and B. Stanton for help in the capture of adult steelhead and advice on raising juvenile fish. S. Latham assisted me in building and running the experiment. The research presented here was evaluated by the Animal Behavior Society's Animal Care Committee and approved on 14 September 1999.

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