Social and spatial structure in brook chars (*Salvelinus fontinalis*) under competition for food and shelter/shade

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ABSTRACT

Salmonids, outside their reproductive period, are seen to have two types of territory called "territorial mosaic" and "partial territory". The first aspect of this research aimed at identifying the type of territory established by mature brook chars in artificial streams. After this, the biological value of spacing out was studied with regard to two resources: food, and shelter/shade which gives protection. Three 5 X 1 X 1 m artificial streams were built on the edge of a natural brook which provided a continuous water supply. One hundred and fifty mature brook chars (Salvelinus fontinalis) taken from that brook were distributed into 30 colonies with 5 members apiece. Three experimental conditions were created, and 10 colonies were submitted to each of these. In the first experimental condition, the quality of shelter/shade differed in 3 sectors of the artificial streams, whereas the quantity of food remained the same for all 3. In the second experimental condition, the quality of shelter/shade was identical, while the quantity of food differed in the 3 sectors. In the last condition, conflict was created: the fish had to choose between an area which offered excellent shelter/shade but no food, one which provided ample nourishment but no shelter/shade, and one in which all those resources were present at intermediate levels. Observation of the 30 colonies revealed "partial territory" in all cases. These corresponded to more or less complete aggressive-dominance hierarchies. Almost every alpha established territory, and the number of territorial individuals progressively decreased throughout inferior ranks. Alphas had exclusive use of their territory. Lower-ranking individuals successfully defended their territory against their subordinates, but were unable to drive away higher-ranking conspecifics. Overall results also indicated that the highest-ranking brook chars in the aggressive-dominance hierarchies more frequently established their territories in sectors of the streams with good shelter/shade than in sectors with good alimentary conditions.

Key-words: spacing out, social space, territory, agonism, dominance, competition for food, shelter/shade, brook char/trout, *Salvelinus fontinalis*.

INTRODUCTION

The use of space by adult salmonids varies greatly according to the season. During the reproductive season, which lasts 2-3 weeks in the boreal area, reproductive individuals occupy and defend very small reproductive territories against adjacent site holders (Fabricius, 1953). The conceptual scheme of territorial mosaic proposed by Greenberg (1947) from his study of immature Lepomis can be applied to the situation: each holder is most of the time successful in chasing out intruders from its defended area, but also respects holding areas of adjacent residents as well. Locus dependent dominance seems to be at the basis of the formation of territorial mosaics and this state of affair, together with putative reversibility, satisfies the criterion for true territoriality, at least of an idealized concept of territoriality. The use of space by juveniles seems to conform to the territorial mosaic scheme in several salmonids (Hartman, 1963, 1965; Hoar, 1951; Kalleberg, 1958; Keenleyside, 1962; Héland, 1971). Jenkins (1969) has suggested that this could be due to the relative uniformity of biophysical and ecological conditions which usually prevail during ontogeny: fish of equal size, age and hormonal development compete against each other over a substrate which is usually also very uniform.

Outside the period of reproduction, adult trouts either form small schools, especially during the winter and under the ice, or hold much larger areas or living quarters (Newman, 1956; Jenkins, 1969; Chapman, 1962; Onodera, 1962). The latter are more or less successfully defended against intrusion and mostly conform to another conceptual scheme, that of Greenberg's partial territory. Resident individuals successfully defend an area against some intruder conspecifics, but not against others. In turn, they may be successful in displacing adjacent residents when invading their territories, especially when these are smaller. Here, dominance relations seem to shape the use of space in an asymmetric but absolute manner. A chase-right dominance structure develops from frequent agonistic interactions of adjacent site holders; one of the consequences of the dominance relation bounding a pair of fish is that the dominant is able, when it invades the subordinate's defended area, to chase the subordinate from its own territory. However, the dominant cannot, in turn, be displaced by the subordinate.

These forms of more or less exclusive use of space are certainly biologically valuable for the individuals showing the behaviour, but surely for different immediate functions. Exclusive use of defended but small nesting areas insures adequate perenniality through possible mate selection, control of nest quality, and evidently direct gene transmission to offspring. The use of larger territories would on the other hand contribute to individual survival through efficient exploitation of alimentary resources, energy conservation (e.g. against strong currents) and defence against predation (Dill et al., 1981; Gibson, 1966; Hartman, 1963; Onodera, 1962; Saunders and Smith, 1962; Symons, 1974).

In the present study we are concerned by the function of large territories occupied outside the reproductive season in the brook char, Salvelinus fontinalis. The first question which is asked is whether space use by brook chars in large artificial streams conforms to more or less strict territorialism as defined above. The second question concerns the relative importance of the various resources which are presumably accessible in a large defended area: which is more important in a territory, access to food or shelter/shade?

METHODS

Subjects

The 150 brook chars (Salvelinus fontinalis) used for this experiment came from the Castor Noir brook alongside which the experimental installations were set. The subjects were captured with a fly casting rod; the barb had been cut from the hook, in order not to wound the subjects. The latter were 10 to 28 cm long, with an average length of 17.1 cm. Their weight varied between 15 and 158 g, 50.35 g on average. 72 males and 78 females were used, respective percentages of 48% and 52%.

Material

The experiment was held over a period of 10 weeks, in June, July, and August 1982. Three artificial streams were created, at the beginning of Summer 1981, near the Castor Noir brook on the Saint-Maurice Reservation, some 80 km from Grand-Mère, Province of Québec, Canada. The streams measuring 490 X 90 X 90 cm were placed parallel to Castor Noir brook (Fig. 1). The base and 3 sides were made of plywood, and the fourth side of two 245 X 85 X 1.6 cm glass panes. The sides of these streams were held together by a soldered angle-iron steel structure. The site of the experiment was approximately 60 m away from a pond that had come to exist following construction of the Castor Noir brook barrage and that had once been used to raise brook char. Gravity brought water from the pond to the first artificial stream through 4 plastic, flexible tubes 6 cm in diameter. Valves maintained velocity of the current between 5 and 10 cm/sec. This was adjusted

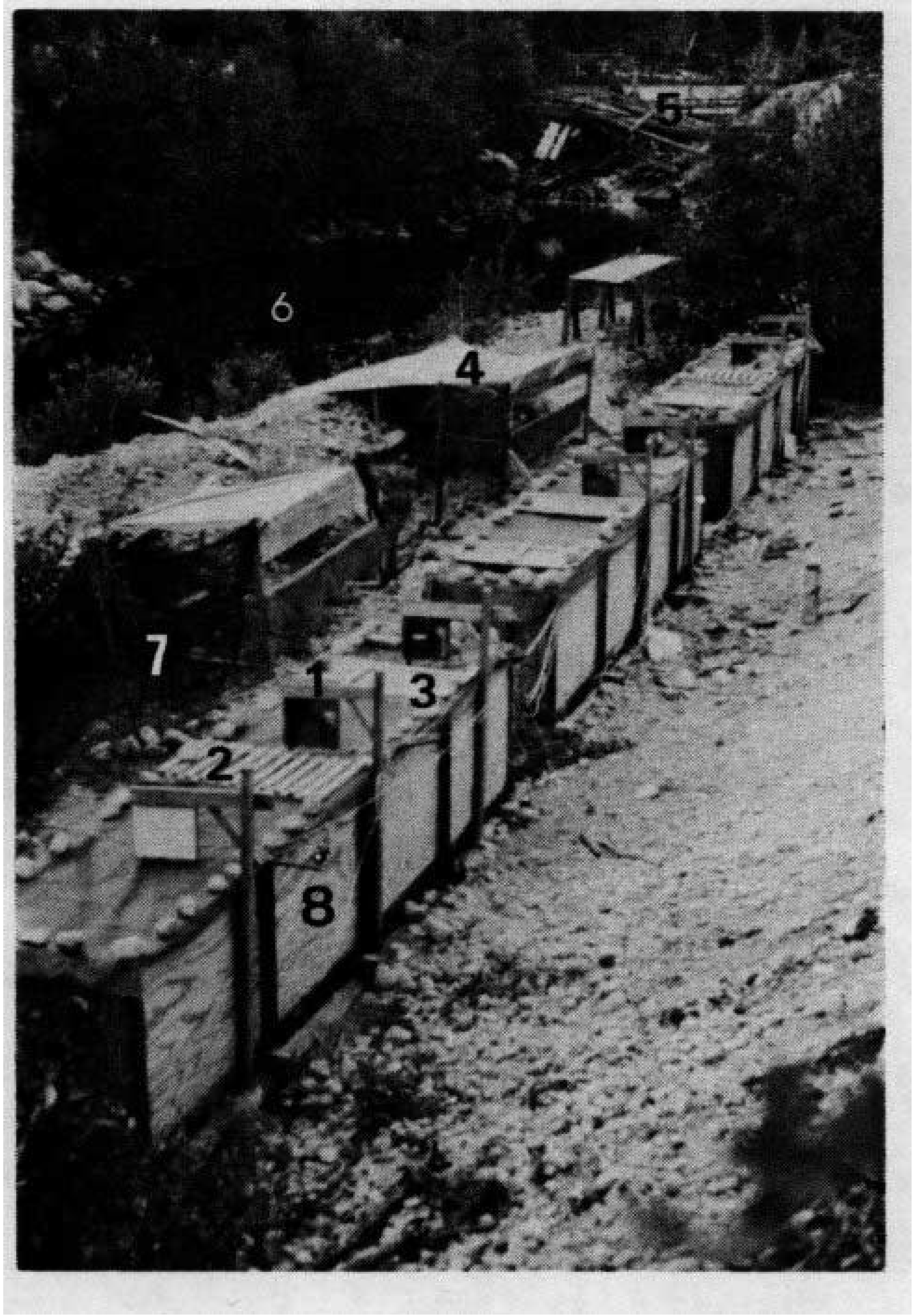

Fig. 1 - General view of the experimental installations. 1- Food distributors. 2- Screen over semi-shaded area. 3- Opaque screen. 4- Observer hideout. 5- Dam and resulting pond. 6- Castor Noir brook. 7- Camouflage net. 8- Artificial stream.

according to the flow in the natural brook. Water temperatures inside the artificial streams varied between 9° and 20°C, 15.7°C on average. In order to avoid predation from mammals and ichtyophagic birds, and to prevent the incoming of any uncontrolled food supplement, the top of each stream was covered with fine wire-netting. The water coming from the natural stream as well as the one flowing from one stream to the other was also passed through filters placed at the mouth of each stream. They were cleaned each day. Finally, in order to avoid food to drift from one section to adjacent ones, stream sections were separated at the surface by 10 cm width mesh deflectors placed at right angle with the water surface. All 3 streams were on the North-South axis. Since they flowed into one another, we felt it necessary to distribute the experimental conditions equally between the 3 streams, through counterbalancing and alternation. In order to heighten luminosity inside the artificial streams, the 3 plywood walls were painted white, using a non-toxic product (International Intergard EHBOOO/1). The inner surfaces of the aquariums were ruled in rectangles. Thirty-six sections, 50 X 45 X 35 cm, were thus obtained and then numbered.

Variables manipulated

Three conditions of shelter/shade were created. These 2 resources were combined so that, in the various experimental conditions, both shelter and shade were at maximum, intermediate or minimum levels.

As concerns shade, the maximum level was obtained by putting a 90 X 50 X 0.5 cm sheet of plywood over a section of the aquarium. This opaque screen, 15 cm above water, provided a totally shaded area (Fig. 1). In the intermediate condition, a semi-shaded area was created by covering an equivalent surface with boards of wood 4 cm wide, set 4 cm apart. The third condition was the absence of cover.

As concerns shelter, the maximum level was obtained by setting 2 cement blocks, 40 X 20 X 10 cm, parallel to one another in the middle section at the bottom of a stream, 25 cm from one another. Two more identical blocks were put at right angles over those first ones, thus creating a refuge for the chars. In the intermediate condition, 2 blocks, identical to those described above, were set in the same fashion, but not covered. The third condition was the absence of shelter.

As for food, 3 levels were also manipulated. Dried crustaceans of the gammaridae family were used. The maximum quantity of food, equal to 1.5% of the (wet) weight of the largest fish in the population studied, was distributed daily. This quantity of food corresponds to the maximum average weight of food which salmonids can eat in one day when fed to satiety in waters at 15^{o}C after having been mildly deprived of food (Elliot, 1975). In the intermediate condition, the quantity of food given out daily was 0.75% of the wet weight of the largest fish which is equal to ½ a maximum daily ration (Elliot, 1975). No food was provided in the last condition. In the case of maximum nourishment, the food was put at the surface of the water 4 times a day, between 08h00 and 18h00, at approximate intervals of 2½ hours. In the intermediate condition, food distribution occurred twice daily, at 5-hour intervals.

Experimental conditions

Three experimental conditions allowed for independent variations in the levels of nourishment, or shelter/shade (Fig. 2). The first experimental condition aimed at identifying the importance of shelter/shade in the choice of a territory. For this purpose, the observer identified 3 sectors in the stream, each comprising three 50 cm-long sections; any resource provided was laid in the middle section of each sector. In 3 of the sections of the 3 streams, the level of shelter/shade varied, while the level of nourishment remained constant at its maximum level. Thus in the first experimental condition, one section offered maximum shelter/shade; in a second section, intermediate levels of shelter/shade were provided; the third section offered no shelter/shade.

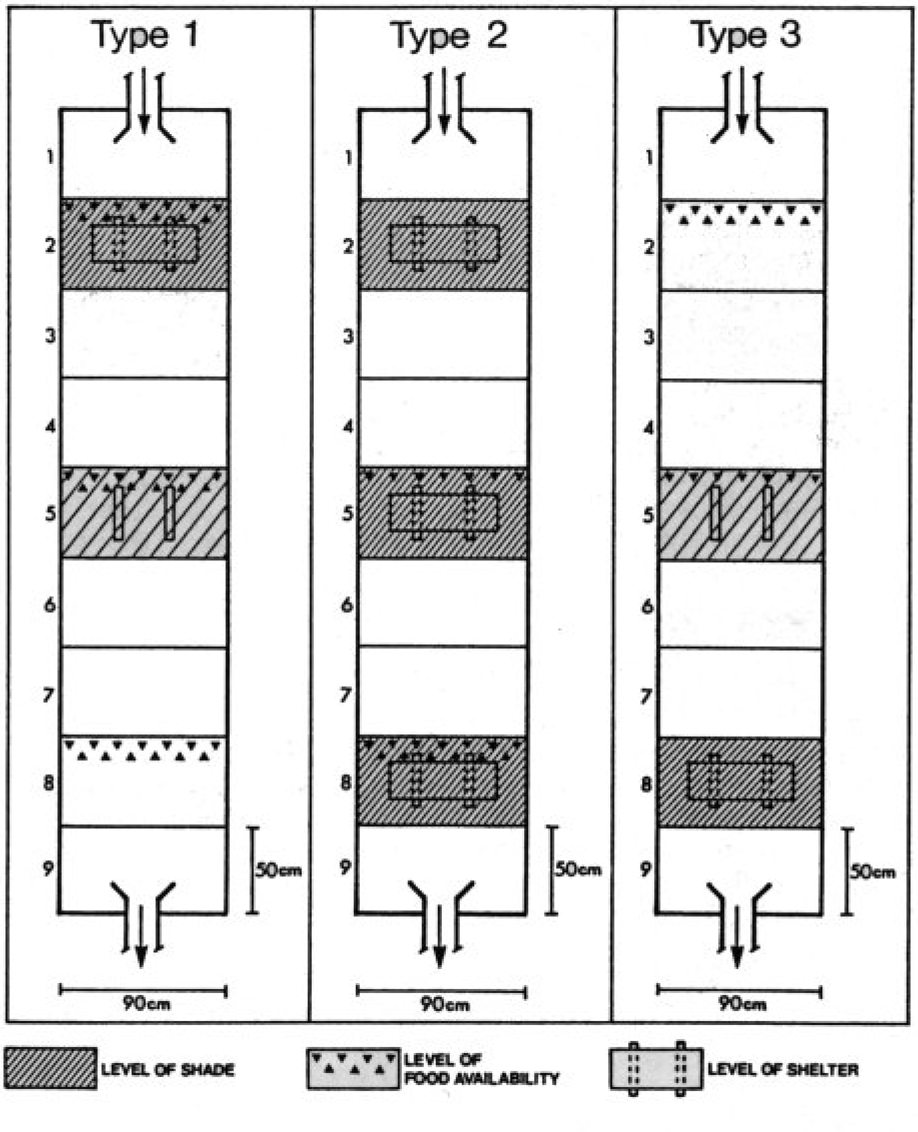

Fig. 2- Schematic representation of the 3 experimental conditions created in each artificial stream.

In the second experimental condition, the levels of shelter/shade were kept constant in all areas, but the level of nourishment varied. The first section provided maximum nourishment, the second one gave the intermediate level of nourishment, and the third offered no food. In the third experimental condition, we varied the availability of both resources in order to estimate the relative importance of each of these when in opposition. In the first section the quantity of food was at maximum, but there was no shelter/shade. In the second section, shelter/shade was at its maximum, but there was no food. The third section offered intermediate levels of both these resources. Ten colonies composed each of 5 fish served under one of each of the 3 experimental conditions. The site of the resource was systematically counterbalanced in the 3 streams, from one week to the other.

Procedures

The experiment was held over a period of 10 consecutive weeks, in the following manner. Fifteen chars were used each week. Immediately after their capture, and following a brief anaesthesia induced by methylpentinol (3 Methyl-1-Pentyn-3 OL) at 2.5 cc concentration per litre of water, subjects were measured and marked. The 15 chars were then distributed evenly into 3 samplings, and each of these subjected to an experimental condition. In order to distinguish between the various subjects in each colony, they had previously been marked using different-coloured pearls. The pearls were sewn onto the adipose fin with a needle and surgical thread. To allow the char to get accustomed to their new environment, and to allow time for the establishment of social and spatial relations observation began only 3 days after the chars had been introduced into the artificial streams. During the following 4-day period, all colonies were then submitted to observation, each of them 2 hours daily. The order in which the 3 colonies were observed was random; the same holds true for the order in which the various chars in each colony were focused. After completion of the observations, the streams were emptied and cleaned in order to eliminate any food that might have remained. The new colonies were then introduced 18 hours later.

Behavioural and spatial observations

A 15-minute focal-animal sampling was done for each fish over 4 consecutive days, for a total of one-hour of observation per fish for each of the 3 colony under observation. The agonistic behaviour of this species has been amply described by Gibson (1978), Newman (1956) and McNicol (1979). Ten behavioural units seemed here relevant. As concerns definitions, the methodology employed in our previous study was here applied (Beaugrand, Caron and Comeau, 1984). Thus the following behaviour units were noted: charge, nip, chase, frontal and lateral display, submissive display, flight, immobility at the bottom, static swimming near the surface, feeding, and sheltering.

In parallel with focal-animal sampling of individual behaviour, a sociometric matrix allowed to note the orders of dominance for the 5 chars in each colony. Non-structured supplementary observation was sometimes necessary to complete the matrix. The sociometric matrices permitted to distinguish between 2 types of aggressive-dominance hierarchies. The first one pertains to orders of dominance between individual subjects for each day of observation. The expression "daily rank" will be used to denote the rank thus obtained. The second type of hierarchy informs on the rank of individual chars for the 4 days of observation. It is obtained by the addition of daily scores; this will be called "weekly rank". In terms of methodology, the weekly rank is of the "nip dominance" type, whereas the daily rank is of the "nip right" type.

The following criterion was applied to identify dominance ("chase right"): an individual was said to be dominant when it attacked, gave pursuit, threatened, or nipped another, and the latter flew or displayed submissive posture 6 consecutive times without countering (Beaugrand and Zayan, 1985).

Since territoriality implies selective occupancy of space, data was gathered on the spatial positions of chars in the streams as an indirect indication of territoriality. The scan sampling technique (Beaugrand, 1984) was used throughout; this consists in taking note of the spatial positions of all chars through visual scanning of the artificial streams, with repetition of the sampling at 15-minute intervals. Thus, 15 scan samplings were done each day, and the position of each char was recorded by noting the sector of the stream where each of them could be seen during a scan. The data used for territory determination were gathered at the same time as the focal-animal sampling. Every colony was thus under observation for 90 consecutive minutes each day. Defended territories were identified and localized using the following criterion: a char was said to have established a territory in one of the 9 transversal sections of the stream when it threatened, charged, nipped or gave pursuit to another char, and the latter fled 6 times from the said section or from adjacent sections. Two observers gathered the data. The Kappa index (Cohen, 1960) was used to establish the degree of interobserver reliability. This produced a Kappa of 0.88 during the experimental phase, and 0.81 during the eighth week.

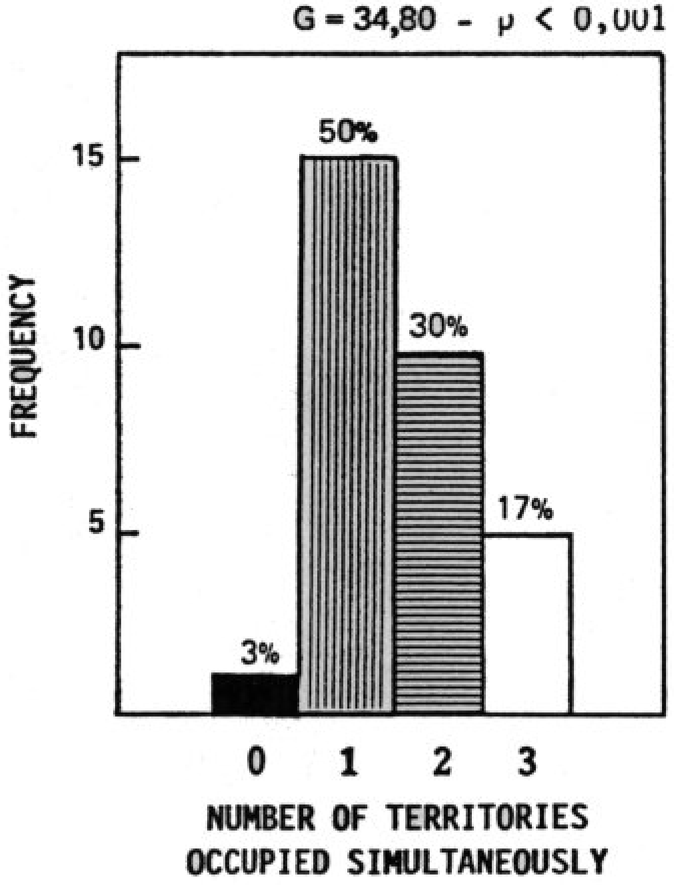

Fig. 3. Frequency and percentage of colonies as a function of the number of territories which were noted simultaneously.

RESULTS

Types of defended territories

Fig. 3 presents the frequency with which one or more territories were noted. In 15 (50%) of the 30 colonies used, only one subject clearly established a territory. In 10 (30%), 2 subjects claimed 2 sites simultaneously; and in 4 (17%), 3 simultaneous territories were established. Never did more than 3 subjects in a given colony manage to establish territory at the same time, and in one colony, no subject met our criterion for territoriality. The likelihood ratio G-test (Sokal and Rolhf, 1969) was applied to see if data deviated from a model of uniform-distribution of territory frequencies. The results show that discrepancies in frequency were not attributable to chance only ($G=34.80$, $p<0.001$). One of the conditions for the existence of a "territorial mosaic" requires that the number of simultaneously defended sites tended in the direction of the number of subjects in the given colony. Instead of this, the present result suggests the reverse: in half the colonies, a single subject managed to establish territory, and the number of colonies in which more than one territory was occupied decreased as the number of simultaneously defended sites increased. The present result does not support the existence of "territorial mosaics" for the species, in the conditions of this study. However, the 3 conditions for "partial territories" were met. It was in fact possible to identify more or less complete structures of aggressive dominance in the 30 colonies on each of the 4 days of observation, except in 2 cases. A larger number of individuals from the higher hierarchic classes defended sites, and the frequency of this declined progressively in the lower hierarchic classes. As shown in Fig. 4, of a possible 30 individuals per rank class, 28 s (93%), 13 ßs (43%), 8 s (26%), and 3 s (10%) defended territories, while no managed to do so ($G=49.64$, $p<0.001$). Overall, intruders of higher rank could chase away residents (territorial individual on its own territory) from the latter's territory, whereas the reverse occurred but exceptionally. Thus a (more) dominant individual chased a (more) subordinate from its own territory on 55 occasions; the reverse was obtained on 4 occasions only ($Z=6.61$, $p<0.001$). Net results therefore seem to confirm the defence of "partial territory" type sites by mature brook chars, when they are put in artificial streams offering unequal conditions of feeding and shelter/shade.

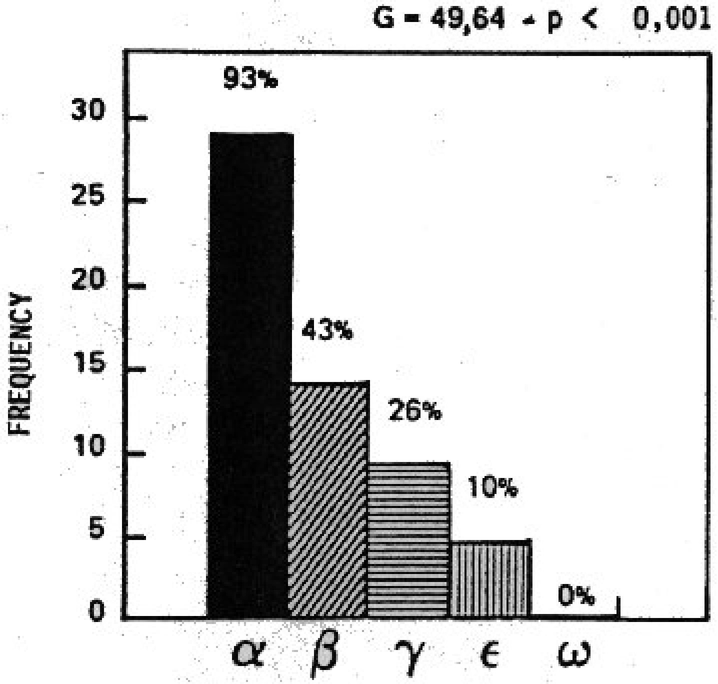

Fig. 4. Frequency and percentage of territorial individuals as a function of their social status.

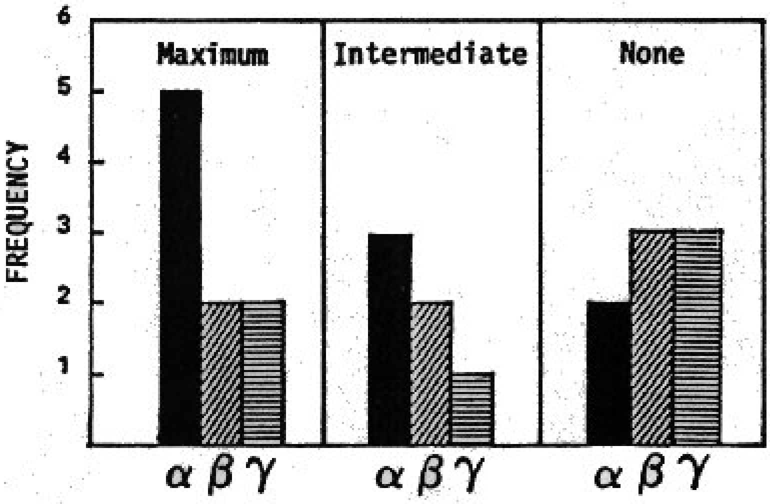

Fig. 5. Frequency of territorial individuals as a function of social status and according to the three levels of shelter/shade.

Territories and resources

In the context of "partial territory", the most dominant individuals in a hierarchy have priority in the establishment of territory. Jenkins (1969) and Newman (1956) had reported this phenomenon for salmonids. The present results corroborate those of the preceding authors. In fact, but for one exception, all s established territory before their lower-ranking conspecifics did. Our analysis of the localization of territory according to resource will therefore mainly focus on the behaviour of s, since the sites settled on by their conspecifics of inferior status are not solely a matter of the latter's preferences: they depend on the behaviour of s. The order of dominance used for the localization of territory is the "daily rank", and the one used for the occupancy of space is the "weekly rank". It must be noted that for s, however, these 2 ranks are the same. The statistical test used for localization of territory was the test for significance of a proportion (Siegel, 1956), and the likelihood ratio test (Sokal and Rolhf, 1969) was used for space occupancy.

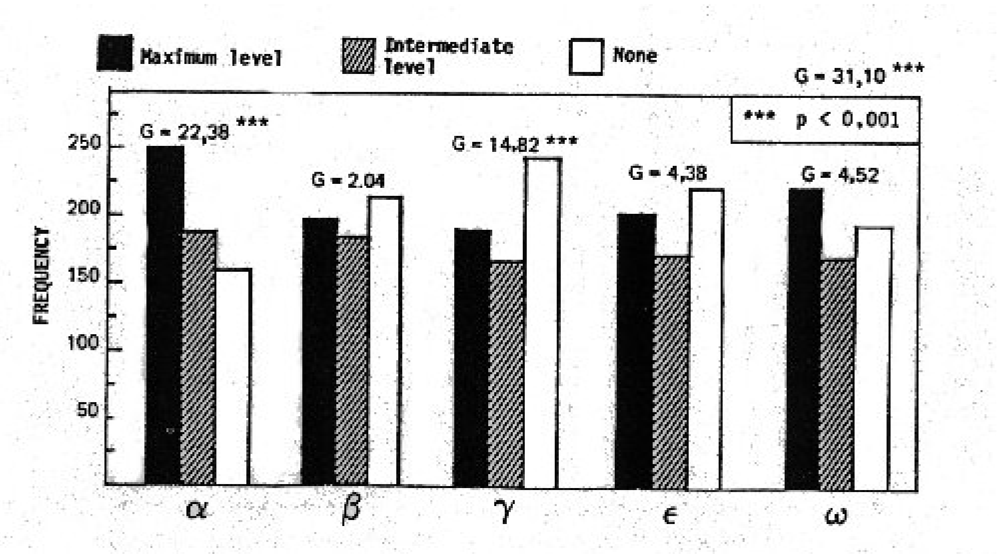

Fig. 6. Frequency of occupancy for the three sectors as a function of social class and the three levels of shelter/shade.

Experimental condition 1. In this experimental condition, the level of food was kept at its maximum in all 3 sectors of the artificial streams, while the quality of shelter/shade varied from one sector to the other. The number of territorial individuals, as a function of rank and varied levels of resource, is shown in Fig. 5. Half the s (5) established territory in sector 1 (maximum shelter/shade), 3 of them held sites in sector 2 (intermediate shelter/shade), and only 2 had their territory in sector 3 (absence of shelter/shade). An assumption of equiprobability in the number of s occupying territory in each of the sections would lead us to expect a proportion of 0.333 subjects in each of the sites. In no sector did the discrepancies between such a model and the data obtained reached significance. It can nonetheless be noted that a greater number of s established territory in the section of the stream which provided most shelter/shade, and that their number decreased where the quality of shelter/shade also decreased. Fig. 6 shows the frequency of occupancy for the 3 sections, as a function of the "weekly rank" of corresponding individuals and the different levels of shelter/shade. Taking all distributions into account, a significant interaction was found to exist between the hierarchic class of individuals and their occupancy of various sectors (G=31.10, p<0.001). Two classes of individuals occupied 3 sectors in a differential fashion: they were all s and s. Alphas were more frequently seen in the sector providing maximum shelter/shade than in the sector where this resource was at intermediate level or in the sector in which it was no-existent (G minimum=9.09, p<0.001). In this latter sector, devoid of shelter/shade, s were found less often than all their subordinates (G min.=4.32, p<0.05). On the other hand, they were seen in the sector where shelter/shade were maximum, more often than all their conspecifics, except s (G min.=5.10, p<0.05).

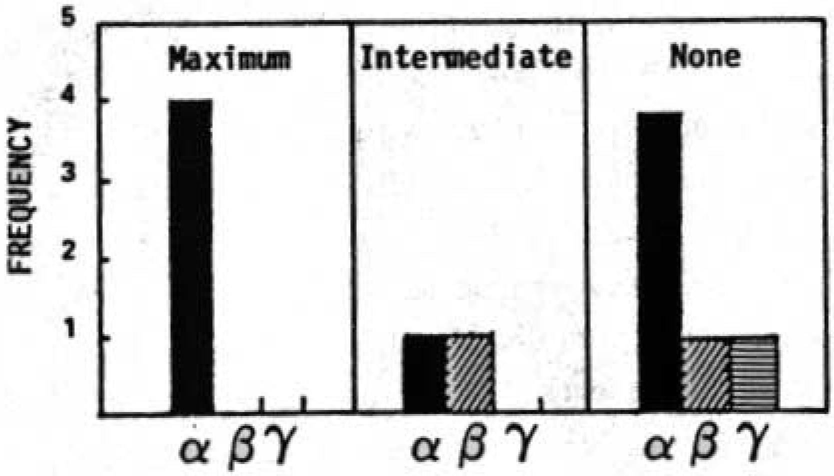

Fig. 7. Frequency of territorial individuals as a function of their social status and the three levels of food availability.

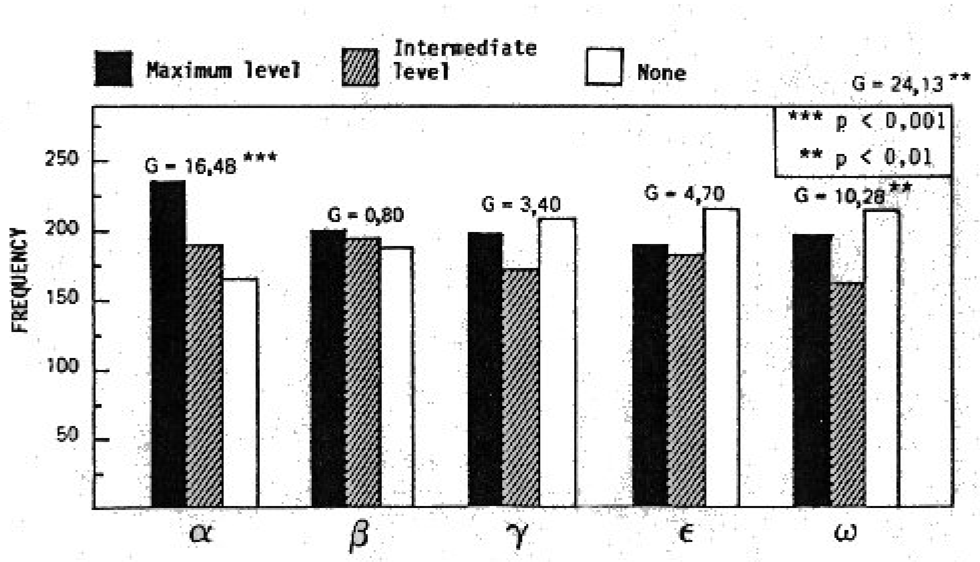

Fig. 8. Frequency of occupancy of the three sectors as a function of social status and food availability.

Experimental condition 2. In this experimental condition, nourishment varied across the 3 sectors of the streams, while the quality of shelter/shade was kept uniform, at its maximum level. The number of territorial individuals as a function of their rank and varying levels of food is shown in Fig. 7. Four s (44%) claimed territory in sector 1 (maximum level of food), 4 again (44%) chose sites in sector 3 (absence of food), and only one (11%) showed territorial behaviour in sector 2 (intermediate level of food). In comparing these data with proportions generated by a model of uniform distribution, it appears that none of the sectors was singled out by the dominant subjects when they established territory. The same number of territorial individuals were seen in the sector without food as in that where food was at maximum level. Fig. 8 shows the frequency of occupancy for 3 sectors in the artificial streams, as a function of the "weekly rank" of the individuals and the different levels of feeding. Taking the distributions as a whole reveals a significant interaction between the "weekly rank" of individual subjects and the frequency of occupancy for the 3 sectors (G=24.12, $p<0.001$). Two hierarchical classes of individuals, s and s, occupied the 3 sectors in a differential fashion. Alphas were seen more frequently in sector 1 than in the 2 other sectors (G min.=4.87, $p<0.05$). Alphas were found in sector 1 more frequently than s or s. And s were found in sector 3 less often than their subordinates (G min.=3.85, $p<0.05$). Results for this experimental condition therefore seem to indicate a preference, on the part of s, for occupancy of the sectors providing a greater degree of nourishment. It must be noted, however, that these sectors also provided maximum shelter/shade. Although s were found more frequently in those sectors, they did not establish territory there more often than in the sectors without food.

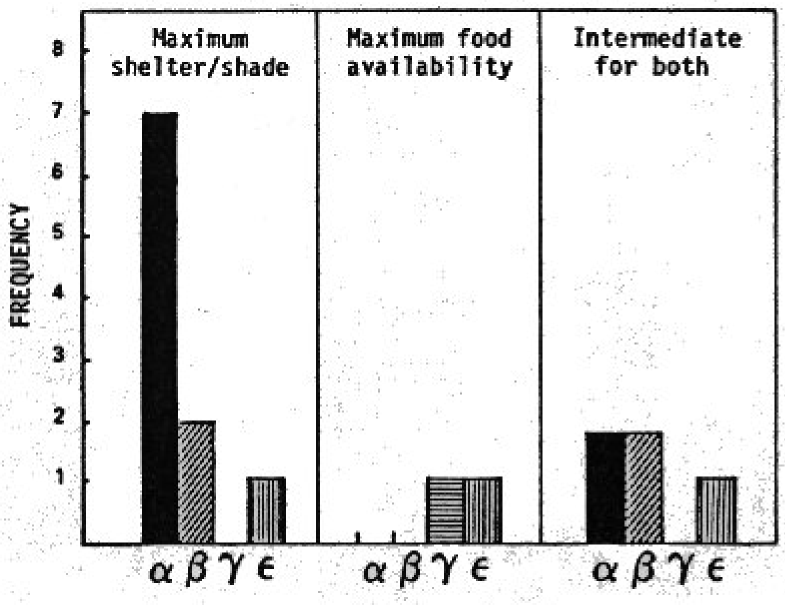

Fig. 9. Frequency of territorial individuals as a function of their social status and available resource levels.

Experimental condition 3. This experimental condition was aimed at determining the relative importance of shelter/shade to that of nourishment, when both resources were opposed. Fig. 9 shows the distribution of territorial individuals according to their rank and to the level of resources. Alphas behaved as follows: 7 out of 9 established territory in section 1 (maximum shelter/shade without food), and this proportion cannot be attributed to chance only ($Z=2.77$, $p<0.01$). No established territory in sector 2 (maximum food without shelter/shade), and a value of $Z=2.08$ ($p<0.02$) reveals a low degree of occupancy by dominants in that area. Also, 2 out of 9 individuals defended a site in sector 3 (intermediate level for both resources); such a proportion does not differ significantly from an uniform distribution. These results suggest that, although they were placed in a conflicting situation between 2 resources, most s occupied space where shelter/shade was at maximum, even if food was absent: no defended space in the section which offered food only. A greater space occupancy was noticed in that part of the stream which provided excellent shelter/shade, than in the 2 other areas. Dominant subjects chose more often the section of the stream where the 2 resources were at intermediate levels than the sector where only food was available. In Fig. 10, the frequency of occupancy for the 3 sections of the artificial streams is shown as a function of the "weekly rank" of individuals and the differing levels of both resources. Overall distribution represents a significant interaction between the hierarchical class of individuals and their frequency of occupancy for the various sections ($G=45.51$, $p<0.001$). Alphas were more frequently found in sector 1 than in sector 2 and 3. They occupied sector 3 more often than sector 2 (G min.=6.56, $p<0.02$). Alphas were found in section 1 more often than any of their subordinates, except for s (G min.=4.39, $p<0.05$). As for section 2, it attracted s more than it did for their subordinates, with the exception of ßs (G min.=3.92, p<0.05). The results obtained in this third experimental condition suggest that s were attracted to the sector providing maximum shelter/shade, although devoid of nourishment, more than they were to the sector where food was at its maximum level, and shelter/shade was non-existent. Alpha occupancy of the sector providing intermediate levels of both resources ranked second. Distinguishing between the different classes of individuals, we found s in the sector providing maximum shelter/shade, although no food, more often than any of their conspecifics, except for s. In the sector providing food only, s were found less often than any of their conspecifics, with the exception of ßs. These results show that shelter/shade was more attractive than food for the dominants in the hierarchy. Also, these results concur with those relating to territorial occupancy by s, since these had a tendency to establish territories in the sections which provided better protection. The results in each of the experimental conditions, as well as the global analysis of these conditions (Caron, 1986), suggest that the quality of shelter/shade had a strong bearing in the defence of sites and occupancy of space by s, whereas food had little bearing on the same. The most dominant chars frequently claimed areas in the streams which provided a greater quantity of food, only if that area also offered superior condition of shelter/shade. Analysis of shelter occupancy by the chars also brings us to grasp the importance of shelter/shade when compared to that of food. Alphas occupied shelters more frequently and for longer periods than all their subordinates. A Wilcoxon test yielded significant discrepancies for both these aspects (Z min.=2.32, p<0.02). Alphas, on the other hand, were no different from their subordinates as concerns their preference for food.

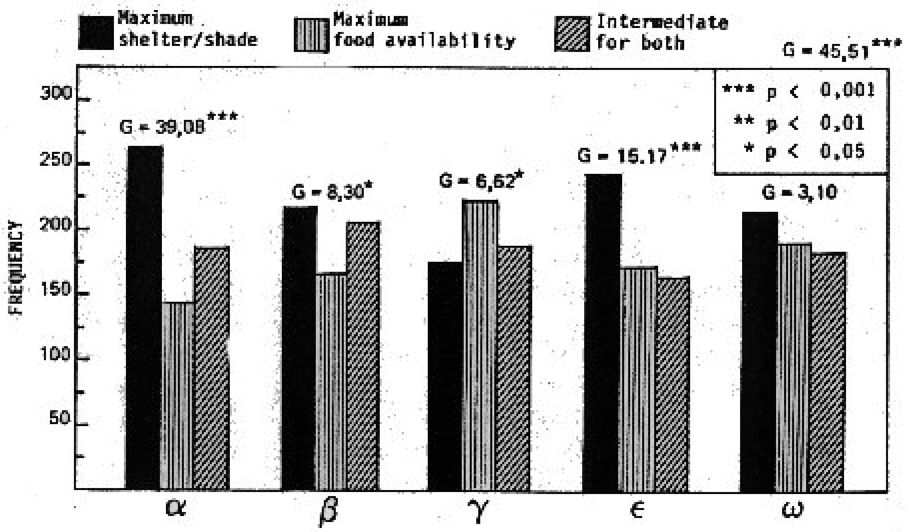

Fig. 10. Frequency of occupancy of the three sectors as a function of the social status and available resource levels.

DISCUSSION

The present results support the hypothesis that the biological value of territorial behaviour for brook chars resides primarily in the appropriation of sites which allow for quality shelter/shade rather than for food. Such results are coherent with many empirical studies on the salmonid family, both in laboratory and in natural conditions. Finding good shelter/shade diminishes the chars' vulnerability to predation, as well as reduce their energy expenditure. Onodera's study (1962) is especially eloquent on the importance of finding shelter against predation. Onodera studied the behaviour of brook chars and rainbow trouts (Salmo gairdneri) in a natural stream, over a period of 3 years. He found 2 factors which explained the death rate of his subjects: predation and floods. Predation was responsible for 97% of deaths in the species. Ichtyophagic birds were responsible for 97% of those losses, while 3% of the young salmonids were eaten by larger conspecifics. Shelter/shade thus appear to have great survival value for the salmonids.

The present study did not systematically control the predation factor, but Mergansers (Mergus merganser), Great blue herons (Ardea herodias) and Ospreys (Pandion haliaetus) were seen quite often near our experimental site. We had to cover the artificial streams with screens, for in the pre- experimental period a Mink (Mustela vison) slipped into the basins. As to the efficiency of the shelters used in this experiment, it became obvious when the experimentators tried to capture the chars after observation. The subjects fled to the shelters, and capture became impossible without lowering the water level and dismantling the shelters.

In all likelihood, there must be fierce competition over these resources, and stronger individuals must be in a position to obtain better protection against predators and heavy currents through site holding and defence. Onodera noted many instances of fights over access to submerged rocks. He also observed that many dominant individuals remained behind such shelters, leaving only nourishment to be sought elsewhere. He gave no quantitative data on this matter. But he did take note of higher rate of survival for larger individuals, which he related to their hierarchical status.

The importance of shelter/shade in providing salmonids with protection against predation has also been noted by Wood and Hand (1985) for the coho salmon (Ocorhyncus kisutch), by McCrimmon (1954) and by Symons (1974) for the Atlantic salmon (Salmo salar), by Saunders and Smith (1962) for the brook char. Salmonids appear also to favour sites which provide good shelter (Gibson, 1966; Hartman, 1963). Hartman (1963) has further shown that brown trouts (Salmo trutta) are more attracted by the double presence of shelter and shade than by either of these 2 resources alone. Shelters not only offer protection against predators and strong currents that may jeopardize the survival of salmonids, they also help reduce the expenditure of energy: by seeking refuge behind submerged rocks, individual salmonids maximize their growth and their potential for adaptation. Hartman (1963) mentioned that brown trouts sought the protection of submerged rocks in artificial streams to a greater degree when current velocity was increased. Héland (1971), in his study of young fish of the same species, noticed that dominant trouts established territory over stream beds with most obstacles and shelters. The same author observed increased growth in dominant and territorial trouts, even though very few dominants established their territory upstream, where food was given out. Li and Brocksen (1977) also mentioned a growth increase in dominant Rainbow trouts (Salmo gardneiri), and noted how they sought sectors of the stream where the current was weaker. Héland (1971) and Li and Brocksen (1977) did not however distinguish between the respective influence of many variables which might explain the higher rate of growth for dominant subjects. In addition to the protection afforded by shelters, which may have contributed to a reduced energy expenditure for dominant subjects, the latter may have been able to benefit from greater nourishment than their conspecifics, but this was not verified in the said studies. However, Metcalfe (1986) re-analyzed the data of Li and Broksen (1977), and showed that the greater growth of dominants was due to both obtaining a greater ration and expending less energy in obtaining it.

The results of the present study on the importance of shelter/shade when compared to food simply suggest that, in the conditions of the present study, food did not appear to be the object of defensive behaviour on the part of the fish. But why ?

Many authors, such as Kalleberg (1958), Keenleyside and Yamamoto (1962), believe the territorial behaviour of the salmonids to be mainly dictated by the need for food. Nonetheless, research on a presumed optimal size of salmonid territory which would be linked to the quantity of food available proved inconclusive (Slaney and Northcote, 1974; Symons, 1971), except when Dill et al. (1981), studying the coho salmon, found a significant inverse relation between territorial size and the quantity of benthic food inside the territory. Yet they were unable to identify the same relation when food was floating above the territories of the subjects. McNicol (1979), for his part, in his research on brook chars, mentioned an increase in territorial size when more food was available. No previous study had up until now experimentally controlled the various resources, in order to test the hypothesis of priority of food over shelter/shade. While experimental control has definitive advantages over correlative studies and especially anecdotical reports, it has nonetheless severe drawbacks on ecological validity. For instance, one can't ignore the possibility that, because they were subjected to capture before the experiment began, the subjects may have been led to intensify their quest for the occupancy and defence of sites that afforded greater protection, rather than quest for food. Latta (1969) has shown that brook chars can support famine-like conditions for several weeks. This great resistance to food deprivation may explain why the chars in the present study did not systematically defend sites which provided most food. It may be that, if the chars had been subjected to famine over a long period, food would have acquired greater incentive importance and driven them to defend sites which provided better nourishment.

Since the fish were fed randomly each day, one might suspect that it was possible to the fish to dash to feeding stations for brief periods to obtain their daily ration, and then to return to their resting positions or shelter. Although observations carried out in the present study were not aimed directly at knowing what happened at feeding time, we nevertheless attest that when food distribution occurred during observation periods, chars were never seen dashing from their initial position to the momentarily active feeding station.

One might criticize also on the fact that the present study did not distinguish between resting and feeding sites as did Fausch and White (1981). These authors have compared brook trout position characteristics before and after brown trout removal, using water velocity difference, proximity of stream bed, being or not under submerged cover, and shade as criteria of quality. Fish holding positions beneath submerged cover which was 15 cm or closer to the stream bed were judged occupying a "resting" position. All other fish positions were classed as occupying a "feeding" position. Although their definitions of "resting" and "feeding" positions are quite questionable, their results agree with the basic regularities found in the present study. After brown trout removal, brook trout larger than 15 cm chose resting positions with more favorable velocity characteristics and more often in shade. "Feeding" positions of brook trout changed little upon brown trout removal. The shift in resting positions of brook chars after release from competition with brown trouts suggested that brown trouts excluded brook trouts from preferred resting positions, the critical and scarce resource.

The criteria used to recognize territorial individual is also extremely important. Let us stress that the present study has used the double criterion of occupancy and active defense. We did not equate the proportion of time spent in different positions with their importance. It is the frequency with which individuals were noted at sampling time in the sector corresponding to a given resource level which was used as an indication of its importance for the animals under study. However, a territory was inferred to exist not merely because of higher site frequentation, as is often the case in ecological studies, but because a given site which was highly frequented was also actively defended by chasing out conspecifics.

The present results on the apparently higher importance of shelter/shade over food can be accounted for by changing priorities. We may be inclined to think that there exists a certain absolute priority between the need for food and the need for protection. But the order of priority for animals depends on momentary or recent physiological needs and ecological conditions. Hypothetically, brook chars and salmonids in general may, in time of famine, seek occupancy of sites with more abundant food first and foremost, since this resource would then favour survival more than would shelter/shade. In other times, though, it may be more adaptive on the part of salmonids to ignore a good meal and avoid becoming foodstuff themselves for a predator. Wilzbach (1985) examined microhabitat use and emigration of wild cutthroat trout from laboratory channels under varying conditions of food abundance and cover. She followed during a week groups of 10 trouts under 4 food-cover combinations (high-high, high-low, low-high, low-low) and constant level of simulated predation risk. Although each treatment was repeated only once (N=2), her results suggest evidence that fish do indeed prefer food to cover when food supplies are only sufficient to maintain short-term survival but not to provide growth. The hypothesis remains to be verified through further experimental research, possibly by submitting the subjects to alternate prolonged periods of feast and fast, all the while manipulating the degrees of predation risk and available cover/shade. Clearly, motivational states and thus priorities can change rather rapidly. They can also be modulated by slow physiological/hormonal processes related to growth and reproduction. For instance, during the ontogenesis of salmonids, the balance between their need for food and their need for protection may be affected by differential imperatives linked to their energy requirements in terms of growth. The daily nutrimental requirement of juvenile salmonids is greater than that of adults ones, proportionally to weight (Elliot, 1975). It is possible, therefore, that the territorial behaviour of juveniles in that family may be under the influence of alimentary needs to a greater degree, and that they first defend sites which offer more from that viewpoint. Since the territories of very young salmonids are only a few centimeters square (Dill, 1978; Le Cren, 1972), many such individuals may regroup to feed in a small perimeter, thus creating the impression of a "territorial mosaic". Proximity may provide protection through the formation of a school (Keenleyside, 1955), when a predator is in pursuit. The differential rate of growth among individuals would eventually contribute to changes of priority, breaking up the "territorial mosaic", and shifting toward "partial territories" instead. The better-adapted individuals would then establish territory where adequate protection be afforded them, in or near sectors where food would also be available. Similar changes in priority probably happens when mature individuals stop feeding and start their migration toward reproductive streams where they will establish and defend territories of the mosaic type. Cultivating such a hypothesis of changing priority could bring about interesting longitudinal research, leading to clarification of many enigmatic aspects of the territorial behaviour of salmonids.

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