Juvenile Territoriality in Stickleback *Gasterosteus aculeatus* L.

Territoriality is a well-known phenomenon among fishes, that is usually associated with breeding territories of reproductive males. Territoriality has also been reported for juveniles in diverse families, ranging from reef-inhabiting fishes in shallow, tropical marine waters (reviewed e.g. in Sale 1978), families that inhabit tropical freshwaters, such as the Anabantoidei (e.g. Tooker & Miller 1980) and Cichlidae (e.g. Wyman & Ward 1973), to families that permanently or temporarily inhabit freshwaters in temperate regions, such as the Salmonidae (reviewed e.g. in Keenleyside 1979). Juvenile territoriality may function as a means of dispersion, with the territories serving as resource territories, i.e. feeding territories (e.g. Slaney & Northcote 1974) and/or shelter against predators (e.g. Symons 1974).

Little attention has been paid to the genetic influence on variation in juvenile territoriality, the exception being a behaviour-genetic study by Ferguson & Noakes (1982, 1983) on the aggressiveness and territoriality of two charr species. Juvenile brook charr, *Salvelinus fontinalis*, are territorial and have high levels of aggressive behaviour, while juvenile lake charr, *S. namaycush*, are non-territorial and rarely show any aggressive behaviour. Using a classical Mendelian cross-breeding design, they showed that the interspecific differences in aggressiveness could be partly ascribed to genetic variation, and that high levels of aggression always coincided with territoriality. The present paper provides evidence for the genetic influence on variation in juvenile territoriality in a fish species from a totally different family that also inhabits freshwaters in temperate regions, the three-spined stickleback, *Gasterosteus aculeatus* L.

Juvenile territoriality in sticklebacks was reported for the first time only recently (Bakker 1986). It may occur as early as 8 weeks after hatching, about 3 weeks after the onset of aggression in groups of juveniles. At that age, fish begin to counter-attack when attacked. Territories occur in groups of different densities, i.e. five and 15 juveniles in 60-litre tanks.

A first indication of a genetic influence on variation in territoriality of juvenile sticklebacks was obtained from lines selected for enhanced or reduced levels of juvenile aggression, called JH and JL lines, respectively (see Bakker 1986). The observations reported here were made on groups consisting of five juveniles (full siblings) from the third selected generation. Each group was produced by a different breeding pair and housed in a 60-litre tank. The tank had three opaque walls with a sand

bottom and a row of long-leafed plants against the rear wall and one of the side walls. The fish were kept at long daylengths (16:8 light:dark) and at a temperature of 18–20°C. During the juvenile phase (from 2 weeks after hatching till sexual maturity of one of the group members, i.e. a period of at least 4 months), the aggressiveness and territoriality of the group (i.e. the number of juveniles defending a territory) was scored in weekly 5-min observations.

Territories were settled first on the bottom, allowing a maximum number of three or four territories. Some of the remaining juveniles defended territories elsewhere in the tank. The criteria for a territory were a defended area with sharp boundaries, in which nearly all intrusions resulted in attacks, after which the territory owner returned to a fixed position. The difference in the level of aggression of JH and JL groups (Bakker 1986) was paralleled by a difference in territoriality; all four JH groups showed frequent territorial behaviour during the juvenile phase, whereas in two out of six JL groups, territoriality was observed on only one occasion (Fisher exact probability test, $P=0{\cdot}07$).

Further indications of a genetic influence on variation in territoriality was obtained by comparing the behaviour of juveniles from two different populations, which were bred from wild-caught parents and reared under similar standardized laboratory conditions (described in Bakker 1986). A comparison was made between laboratory-bred and -raised juveniles from an anadromous (A) population collected at Den Helder (Netherlands) and a freshwater (F) population collected from a trout hatchery in Emst (Netherlands). The latter fish belong to the same population that was used for the above-mentioned selection experiments. Groups of five juveniles (full siblings), each from a different breeding pair, were housed in 60-litre tanks and scored weekly for their aggressiveness and territoriality in 5-min observations.

The A groups displayed lower levels of aggression than the F groups (Bakker, Feuth-de Bruijn & Sevenster, unpublished data; see Goyens & Sevenster 1976). This was accompanied by a lower tendency to show territorial defence in A groups than in F groups (Fig. 1); in 12 out of 25 A groups we never observed territorial behaviour, whereas in only one F group out of 26 was territoriality absent (χ^2, test two-tailed, $P<0{\cdot}001$). Moreover, in those groups that showed territorial behaviour, the maximum number of territories observed was on average greater in F groups than in A groups: 4·2 versus 2·6 (Mann–Whitney *U*-test, one-tailed, $P<0{\cdot}001$). The maximum number of territories observed was unrelated to and even exceeded the number of juvenile males in the group, as established histologically afterwards.

With respect to juvenile behaviour, some interesting parallels can be drawn between the salmonids and the three-spined stickleback. Juvenile territoriality is found among those salmonid species that spend the first months or years of their lives in running water (rivers and streams), such as the Atlantic salmon, *Salmo salar*, the coho salmon, *Oncorhynchus kisutch*, and the brook charr, *Salvelinus fontinalis*. This contrasts with species that migrate to the sea soon after hatching, such as the pink salmon, *Oncorhynchus gorbuscha*. Juveniles of these species have very low or zero levels of aggression and live in shoals (reviewed in Keenleyside 1979). Shoaling with the absence (or low level)

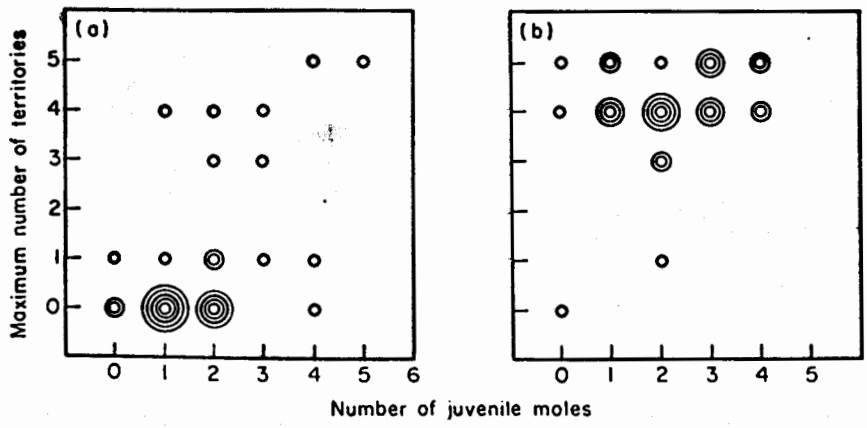

Figure 1. Juvenile territoriality (expressed as the maximum number of territories observed) as a function of the number of juvenile males in groups composed of five juveniles from (a) an anadromous (25 groups) and (b) a freshwater (26 groups) population. Each circle represents a group of five juveniles.

of aggression and territorial behaviour is likely to be an adaptation to their juvenile migratory behaviour, in which shoaling serves as an anti-predator device (reviewed in Pitcher 1986). Three-spined sticklebacks of anadromous populations start to migrate to the sea at an early age (about 5 weeks after hatching) in more or less large shoals (e.g. Daniel 1985).

Except for reproductive males, practically nothing is known about territoriality in sticklebacks. Field observations by MacLean (1980) on a freshwater population suggested that sticklebacks may maintain feeding territories outside the breeding season. The present finding that juvenile territoriality is not confined to one sex, just like juvenile aggressiveness (Bakker 1986), agrees with the notion that juvenile territories may function as resource territories. In other fish species that show juvenile territoriality, this independence of sex has been assumed implicitly, but little effort has been made to verify it.

The diversity of freshwater populations of sticklebacks with respect to biotic and abiotic factors offers ideal material for further research on the selective forces shaping territoriality in this species, which may be guided by the salmonid research on juvenile territoriality.

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