VARIATION IN SCHOOLING AND AGGRESSION AMONGST GUPPY (POECILIA RETICULATA) POPULATIONS IN TRINIDAD

by

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(With 7 Figures)
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Introduction

Schooling behaviour offers fish an effective defence against many types of predators (MAGURRAN, 1990). The enhanced vigilance of larger groups means that approaching predators are more readily detected while information transfer amongst school members ensures that all individuals rapidly become aware of impending danger (MAGURRAN & HIGHAM, 1988). If an attack is escalated, the confusion effect, in conjunction with a range of escape tactics, helps reduce the predator's chance of success (NEILL & CULLEN, 1974). Many of these responses rely on uniformity of morphology and behaviour. For example, the confusion effect is most successful when all group members are of similar size (THEODARKIS, 1989) and appearance (OHGUCHI, 1981; LANDEAU & TERBORGH, 1986) while highly organized manoeuvres, such as the fountain effect and the flash expansion, depend on coordinated behaviour. There is also some evidence that, under certain conditions, pairs of sticklebacks, *Gasterosteus aculeatus* (MILINSKI, 1987; MILINSKI *et al.*, 1990a, 1990b) or guppies *Poecilia reticulata* (DUGATKIN, 1988) opt for cooperative alliances (using the Tit for Tat strategy) during predator inspection. Inspection behaviour occurs when individuals or small groups approach a potential predator

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in order to obtain information on its identity or behaviour (MAGURRAN & PITCHER, 1987). As LAZARUS & METCALFE (1990) point out, it is difficult to distinguish true cooperation from the apparent cooperation arising from the safety in numbers advantage of schooling.

The uniform nature of fish schools led early workers (for example RADAKOV, 1973) to view them as egalitarian societies that had evolved through group selection. Evolutionary biologists no longer subscribe to this idea and recognise instead that individual fish must achieve a compromise between cooperative and competitive behaviour (HUNTINGFORD & TURNER, 1987). This arises from the fact that the very uniformity of behaviour crucial to the success of schooling as a defensive tactic has to be reconciled with the need to compete for limited resources such as mates or food. Evidence for a potential cost to schooling behaviour is provided by the observation that there is intraspecific variation in schooling tendency. For example, levels of schooling behaviour are reduced in populations of guppies (SEGHERS, 1974; LILEY & SEGHERS, 1975) and European minnows, *Phoxinus phoxinus* (MAGURRAN & PITCHER, 1987) where predation pressure is low.

Individual fish may switch between aggression and schooling. For instance, when White Cloud Mountain minnows, *Tanichthys albonubes*, explore a new environment, they initially form well-coordinated schools from which males defect to set up defended territories near clumps of weed (MAGURRAN & BENDELOW, 1990). Aggressive interactions are also observed in bluntnose minnows, *Pimephales notatus*, and European minnows, particularly when hunger levels are increased (MORGAN, 1988) or feeding sites are limited (PITCHER *et al.*, 1986). Nevertheless, given the fundamental incompatibility of agonistic behaviour and schooling behaviour it seems likely that selection for schooling will lead to a reduction of aggression. This paper utilises the well documented variation in the schooling tendency of Trinidad guppy populations to test the hypothesis that levels of individual aggression will be lower in populations where schooling is well-developed in response to predation pressure. Laboratory populations and inter-population hybrids are also employed to examine the inheritance of aggression and to exclude the possibility that aggression is an artifact of overcrowding in small aquaria.

The guppy is a small poeciliid fish native to NE South America and the adjacent islands. In Trinidad, where the species is abundant and widely distributed, guppies are exposed to a variety of predation regimes. In some rivers, particularly those draining the northern slopes of the Northern Range, guppies are sympatric with freshwater prawns in the