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การอยู่เป็นฝูงและปัจจัยที่มีผลต่อองค์ประกอบของฝูงปลา

Shoaling and Factors Underlying Shoal Composition in Fish

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บทคัดย่อ

บทความนี้ทบทวนเรื่องการอยู่กันเป็นกลุ่มในสัตว์โดยเน้นไปที่พฤติกรรมการอยู่เป็นฝูงในปลา ซึ่งให้ภาพรวมโดยทั่วไปของความรู้ที่เกี่ยวกับพฤติกรรมการอยู่เป็นฝูง ข้อเสียและข้อดีในการอยู่เป็นฝูง ปัจจัยที่อาจมีผลต่อองค์ประกอบของฝูงหรือมีอิทธิพลต่อการตัดสินใจของปลาแต่ละตัวในการที่จะร่วมฝูงใดฝูงหนึ่ง ซึ่งปัจจัยเหล่านี้ได้แก่ ชนิด เพศ การแบ่งตามฟีโนไทป์ ภาระทางปรสิต ความคุ้นเคยและความเป็นเครือญาติ

ABSTRACT

This article reviews group-living of animals, by focusing on shoaling behaviour in fish. It provides a general overview of shoaling behaviour, costs and benefits of this behaviour, and also factors which may underlie shoal composition or influence the decision of an individual to join a shoal. These include species, sex, phenotypic assortment, parasite load, familiarity and kinship.

คำสำคัญ: พฤติกรรมการอยู่เป็นฝูง การอยู่เป็นฝูงในสัตว์ ปลา

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Shoaling behaviour

Shoaling is a behaviour of fish in which they remain together through social attraction (Pitcher and Parrish, 1993). This behaviour is widespread among fish species and it has been estimated that over 50% of approximately 25,000 species of fish engage in shoaling at least at one point of development during their ontogeny and around 25% of fish species shoal throughout all of their lives (Shaw, 1978). Such groups range from small aggregations of small groups of cyprinid fishes in freshwater habitats to huge pelagic groups of marine fishes such as cod, herring or tuna. Because of the existence of enormous shoals of marine fishes, shoaling contributes to the commercial importance of fisheries (Shaw, 1978; Parrish, 1999). Fish shoals have also attracted biologists, especially behavioural ecologists, because they are model systems to investigate several aspects of social behaviour and organisation (Krause and Ruxton, 2002). Shoaling in freshwater fishes has been studied more often than shoaling in marine species, probably because pelagic fish move fast and usually form vast groups. This makes direct observation difficult and the capture of complete shoals impossible in the wild. In contrast these constraints are reduced in freshwater fishes (Krause et al., 2000).

A definition of shoaling has been the subject of some debate and confusion in the literature exists between shoaling and the term schooling (Shaw, 1978; Pitcher, 1983; Paxton, 1996; Griffiths and Magurran, 1999; Croft et al., 2003). The term ‘shoal’ is commonly used to refer to any social aggregation of fish, whereas ‘school’ refers more specifically to a polarised group of fish, defined by synchronised swimming behaviour (Pitcher, 1983; Smith, 1997). Also, ‘school’ is used to refer to a subcategory of ‘shoal’ (Smith, 1997). Therefore, the term ‘shoal’ is used as an inclusive term to define a functional aggregation of fish that may or may not be polarized in order to be consistent throughout this thesis.

The costs and benefits of shoaling behaviour

Shoaling behaviour involves both costs and benefits to individuals, the most important of which are considered to be related to foraging and the avoidance of predation and are considered to arise as a result of trade-offs made by individuals within a group (Pitcher and Parrish, 1993). However, there are other costs and benefits of shoaling to be considered (Krause and Ruxton, 2002). The followings are brief summaries some of the advantages and disadvantages of shoaling.

There are many potential benefits of shoaling as reviewed in Krause and Ruxton (2002). These benefits include anti-predator protection, foraging and reduced cost of locomotion. The anti-predator benefits include improved predator detection, attack dilution, confusion and predator evasion. Consequently, individuals in shoals are safer than solitary fish. Even though predators preferentially attack large shoals, predator hunting success decreases with increasing shoal size (Krause and Godin, 1995). Shoaling also provides foraging benefits. Individuals within a shoal are able to locate food more swiftly than when solitary (Ranta and Juvonen, 1993) and are able to gain access to defended resources (Foster, 1985). Additionally, shoaling individuals are able to devote more time to foraging (Magurran and Pitcher, 1983), as they reduce the time spent scanning for predators (Caraco, 1979). Ancillary benefits to shoaling behaviour in terms of reduced costs of locomotion are the hydrodynamic advantages of swimming in a group. It was found that, due to utilisation of vortices, there were reduced tail-beat frequencies and thereby energy saving accruing to individuals in groups as opposed to solitary individuals (Herskin and Steffensen, 1998).

When considering potential costs, larger groups are more apparent to predators because of increased conspicuousness. There is evidence from laboratory experiments that fish predators showed a preference for larger groups when offered a choice between two groups, differing only in size (Krause and Godin, 1995). Increased attack rate of predators on fish prey is also found because of the oddity effect. By using shoals of eight minnows, Landeau and Terborgh (1986) discovered that bass capture success was very low in mono-coloured shoals whereas in mixed-coloured shoals, the capture success of the bass increased dramatically when one colour type was in the minority and this type of minnow was caught by the bass at the highest rate. This oddity effect also applies to body size and incurs costs to fish prey by increasing capture success of predators (Theodorakis, 1989). Finally, there is a cost of shoaling behaviour when foraging, because of competition for resources. There is evidence of competition among three-spine sticklebacks (*Gasterosteus aculeatus*). Individuals prefer smaller shoals after they were food-deprived (Krause 1993). Similarly, it was found that food-deprived killifish (*Fundulus diaphanous*) spent more time alone and less time shoaling than non-deprived fish (Hensor et al., 2003). This suggests that state of hunger may affect the decision to join a shoal.

Factors underlying shoal composition

There are a number of factors which may underlie shoal composition or influence the decision of an individual to join a shoal. These include species, sex, parasite load, familiarity and kinship which are described in more details below.

Species (conspecific vs. heterospecific)

A preference for conspecifics over heterospecifics has been reported in a number of teleost species as reviewed in Krause et al. (2000). An early study on this subject found that threespine sticklebacks showed a preference for conspecifics when the heterospecific stimulus fish were bitterling, but not when roach were used (Keenleyside, 1955). The functional significance of preferring to group with conspecifics is likely to be due to two main factors. By associating with conspecifics an individual reduces its chances of suffering the increased predation risk of the oddity effect. A similar case can be made for foraging behaviour. The probability of detecting suitable food is likely to be maximised in the company of conspecifics that have similar dietary preferences (Krause and Ruxton, 2002). However, fish showed no preference for conspecifics when considering the effects of familiarity. It was found that chub (*Leuciscus cephalus*) demonstrated a preference for familiar heterospecifics of minnows (*Phoxinus phoxinus*) instead of non-familiar conspecifics (Ward et al., 2003).

Sex

The sex composition of shoals may influence shoal choice decisions both in terms of mating choice and shoaling behaviour. Previous studies on Poeciliid fishes with polygamous mating systems have described that mate choice may determine association patterns. The sailfin molly (*Poecilia latipinna*) showed that females prefer larger males over smaller males (Witte and Ryan, 1998). However, a later study found that the preference for larger individuals in sailfin mollies existed both within and between the sexes (Gabor, 1999). This finding suggests that natural selection for this species favoured the observed association patterns not only for mate choice but also for a variety of conditions such as predation pressures and shoaling behaviour. Sex composition of a shoal may influence shoal choice decision when considering genetic relatedness of individuals in the shoal. In the rainbowfish (*Melanotaenia eachamensis*) it was found that females preferred to shoal with unrelated males rather than their own brothers. However, the females preferred to shoal with female relatives and only avoided male relatives (Arnold, 2000). This study suggests that females are able to discriminate male relatives and show no preference to kin of the opposite sex to avoid inbreeding. Recently, it has been demonstrated that sex differences may be a factor underlying shoal choice decision in zebra fish (*Danio rerio*). By giving choices of shoals that differed in sex to focal fish, it was found that males preferred to associate with female shoals over males shoals, but no preference was found when a mixed-sex shoal was presented as the alternative. However, females showed no preference when given a choice between male and female shoals (Ruhl and McRobert, 2005).

Phenotypic assortment

Association preferences for fish of similar phenotype have been found in several studies in the laboratory, especially assortment for body length and colour as reviewed in Krause et al. (2000). This can occur both when shoal-mates are conspecific and when they are heterospecific. By associating with individuals with similar phenotypes, fish may maximise their individual fitness by minimizing the cost of both competitive asymmetries and oddity related predation risks (Ranta et al., 1994). In addition to the influence of the phenotypes of shoal mates on shoal choice decisions, the surrounding environment also has an effect (Bradner and McRobert, 2001). This study on assortment of body colouration in mollies (*Poecilia latipinna*) found that when black individuals of mollies, were given the choice between two black shoals (i.e. consisting of black individuals), one on a black background and the other on a white one, more time was spent with the shoal on a black background, Similarly, when given the choice between two white shoals, black-coloured fish spent significantly more time with those that had a black background. In the wild, there was evidence that free-ranging shoals are assorted by body length as well (Krause et al., 1996; Hoare et al., 2000; Croft et al., 2003). These studies supported observed patterns of laboratory studies that found a strong preference for sized-matched individuals.

Parasite load

Due to the confusion in the use of the terms of parasites and pathogens through the literature, parasites are used throughout to refer to living organisms infecting fish both internally and externally. These infectious endoparasites and ectoparasites of fish include viruses (Whittington et al., 1999), fungi (Ward et al., 2005), protozoa (Kolesnikova, 1994) and worms (Krause and Godin, 1994; Barber and Huntingford, 1995; Blake et al., 2006; Seppala et al., 2008; Tobler and Schlupp, 2008). These parasites have been shown to have an effect on shoaling behaviour and foraging ability as reviewed in Barber et al. (2000). Therefore, it is expected that species avoidance of parasitised individuals has evolved, which may explain the occurrence of parasite-assorted shoals in the field (Hoare et al., 2000). Parasitised fish are found more often in peripheral shoal positions and show a reduced tendency for shoaling in some fish species (Barber et al., 2000). Even though the risk of infection is an obvious cost of association, there might be a trade-off with a benefit such as foraging success. By capturing entire shoals of the banded killifish (*Fundulus diaphanus*) in the wild with an ingenious technique using a grid net that maintained the positions of individuals within shoals, it was found that individuals in the front section of a shoal tended to be not only larger than those in the rear section, but also parasitised by the digenean trematode (*Crassiphiala bulboglossa*). In addition, parasitized fish were also found more in peripheral positions than central ones in a significant number of shoals (Ward et al., 2002). In the binary choice test in the laboratory in the same species, it was found that the relative shoaling preference of unparasitized individuals for unparasitized shoals increased with increasing degree of parasite load in parasitized stimulus fish. This finding may imply that parasitised shoal-mates may attract predators because of an oddity effect or may generally be of low quality in terms of shared anti-predator benefits such as predator detection (Krause and Godin, 1994).

Familiarity

Several studies have demonstrated that fish are capable of individual recognition. Therefore, shoaling decisions may be based on previous experience with other members of the shoal and several studies have reported shoaling preferences for familiar fish (see review in Krause et al. (2000)). Shoaling preference for familiar individuals may also have important adaptive benefits. In an experiment using fathead minnows (*Pimephales promelas*), it was found that in response to a predation threat from northern pike (*Esox lucius*), the rate of predator inspections and the numbers of inspectors per inspection was greater in shoals consisting of familiar individuals in comparison to unfamiliar ones and the minnows in groups that were familiar showed greater shoal cohesion than in unfamiliar groups (Chivers et al., 1995). An increase in shoal cohesion may not only result in increased anti-predator success but foraging benefits may also exist for associating with familiar individuals (Swaney et al., 2001). Furthermore, it may be of benefit for individuals to know the competitive ability of others and this may reduce levels of aggression. Metcalfe and Thomson (1995) showed that European minnows (*Phoxinus phoxinus*) could discriminate between shoals of poor competitors (with prior experience) and shoals with good competitors (without prior experience) by preferring to shoal with fish of low competitive ability. In an investigation of levels of aggression on juvenile sticklebacks, Utne-Palm and Hart (2000) found that pairs of individuals that were familiar showed lower levels of aggression when sharing a common food source in comparison to pairs of non-familiar individuals.

Kinship

Benefits of associating with kin may include increased inclusive fitness among shoal-mates (Pitcher and Parrish, 1993; Ward and Hart, 2003). Decision-making to shoal with kin may be important in the evolution of co-operative behaviour (Dugatkin, 1997). There is the evidence of kin recognition in a number of fish species (Arnold, 2000; Hiscock and Brown, 2000; Frommen and Bakker, 2004; Frommen et al., 2007; Hain and Neff, 2007). However, if all test fish were reared in kin groups, these results may be due to preference for familiar odours rather than an innate kin recognition mechanism (Krause et al., 2000). Investigations on guppies revealed that familiarity took approximately 12 days to develop (Griffiths and Magurran, 1997). Hain and Neff (2007) separated the juvenile guppies within 24 hours of birth. Consequently, the finding of kin recognition in guppies in this study should not have been outweighed by familiarity. Investigation of kin recognition of fish has mainly focused on salmonids using young fish and previous studies have shown that salmonids are able to recognise kin (Olsen et al., 2004). Combining rearing experiments in the laboratory and the advanced tagging of fish in the wild, using passive integrated transponders (PITs), it was found that siblings swim spatially closer than unrelated fish during their seaward migration as smolts, supporting the hypothesis that smolts migrate in kin-structured groups (Olsen et al., 2004). It can therefore be seen that there is reliable evidence for kin recognition or kin preference both in the laboratory and in semi-field conditions. However, difficulties exist in detecting kinship in the wild because it is essential to capture an entire shoal to come to firm statistically- testable conclusions, and to use highly informative genetic markers (Krause et al., 2000). Furthermore, to analyse the data with the appropriate statistics to detect kinship is of crucial importance (Luikart and England, 1999). Taking into account these three problems in the past, it is difficult to find kin assortment in fish shoals in the wild; however, Piyapong et al. (2011) shows this existence in the wild guppies.

In conclusion, studying shoaling behaviour and factors underlying shoaling composition may have important implications for understanding population viability, gene flow, and the management of and protection of commercially important, domesticated and endangered fish species. For example, by removing potential predators from an ecosystem, it will not only have an effect on shoaling behaviour, but also the genetic structure of the prey groups.

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