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The Effect of Hunger on Shoal Choice in Golden Shiners (Pisces: Cyprinidae, *Notemigonus crysoleucas*)

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Abstract

When an animal has a choice of joining one group over another, its decision may depend on its relative vulnerabilities to predation and starvation. For example, a well-fed animal may choose a large group of individuals with body size matching its own because this gives good protection against predators, but a hungry animal may prefer smaller groups made up of smaller individuals because this decreases food competition. To test this idea, a choice between various shoals was given to golden shiners, *Notemigonus crysoleucas,* that were either well fed or deprived of food for 48 h. In a choice of 10 vs. 3 shoalmates, both well-fed and hungry shiners spent more time near the shoal of 10. In a choice of 20 vs. 3 shoalmates, both well-fed and hungry shiners again preferred the larger shoal, but in one replicate this preference was significantly weaker in the hungry fish. This reduced preference did not appear to be an artefact of increased mobility by hungry fish searching for food. In a choice between shoals of small vs. large conspecifics, small well-fed shiners, small hungry shiners, and large well-fed shiners preferred shoalmates with body size matching their own, but large hungry shiners preferred smaller individuals. These results are consistent with the hypothesis that hungry fish sacrifice safety from predation in their shoaling behaviour (by avoiding larger groups to a certain extent and by risking the oddity effect) so as to decrease food competition.

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Introduction

Living in groups has benefits and costs (PULLIAM & CARACO 1984; PITCHER & PARRISH 1993). Benefits include reduced predation risk (because of increased overall vigilance, attack dilution, and predator confusion or deterrence) and higher rates of food discovery. Costs include increased competition for resources, food in particular, and higher rates of disease transmission. In situations where an animal must decide whether to join a group or not, and what kind of group to join, benefits must be weighed against costs.

The extent of the benefits and costs associated with group living can be influenced by various factors, some of which are inherent to the group being joined, while others relate to the individual joining the group. Group factors have been especially well studied in fish, probably because it is easy to manipulate shoal parameters under controlled

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conditions. In fish, group factors that have been shown to influence shoal choice include the number (KEENLEYSIDE 1955; HAGER & HELFMAN 1991; ASHLEY et al. 1993), dominance status (METCALFE & THOMSON 1995), food-finding ability (DUGATKIN & WILSON 1992), foraging behaviour (PITCHER & HOUSE 1987; RYER & OLLA 1992), reproductive status (VAN HAVRE & FITZGERALD 1988; LINDSTROM & RANTA 1993), parasite load (DUGATKIN et al. 1994; KRAUSE & GODIN 1996), species similarity (WOLF 1985; ALLAN & PITCHER 1986), size similarity (PITCHER et al. 1985, 1986; RANTA et al. 1992a,b; KRAUSE 1994; KRAUSE & GODIN 1994), kinship (QUINN & BUSACK 1985; VAN HAVRE & FITZGERALD 1988; FITZGERALD & MORRISSETTE 1992; BROWN & BROWN 1996), and familiarity (BROWN & COLGAN 1986; BROWN & SMITH 1994; MAGURRAN et al. 1994) of group members. Individual factors, which have received much less attention, include vulnerability to either predators, parasites (KRAUSE & GODIN 1996), diseases, or starvation (hunger).

Individual and group factors can interact in an individual's decision to join one group over another. For example, well-fed threespine sticklebacks, *Gasterosteus aculeatus*, prefer to join the larger of two shoals, presumably because of increased protection against predators, but hungry sticklebacks either decrease this preference (KRAUSE 1993) or reverse it (VAN HAVRE & FITZGERALD 1988), presumably because hungry fish are more sensitive to the higher competition for food that larger shoals create. Similarly, European minnows, *Phoxinus phoxinus*, and threespine sticklebacks reduce their general shoaling tendencies when they are hungry or weakened by parasites (BARBER et al. 1995).

In this study we used a shoaling cyprinid fish, the golden shiner, *Notemigonus crysoleucas*, to further document the interaction between hunger (as an individual factor) and two group factors, namely the number of group members (shoal size) and their relative body size. In the case of shoal size, we attempted to replicate KRAUSE's (1993) above-mentioned results with a species other than threespine sticklebacks, and with the following additional consideration: we closely monitored the behaviour of the choosing fish, and especially its mobility, to address the possibility that apparent decreases in shoal preference by hungry fish may be a simple consequence of increased movement (induced by a search for food) rather than a change in true shoal preference (KRAUSE 1993). Finding an increase in movement and in foraging behaviour concomitant with a decreased preference for larger shoals by hungry fish would have important consequences for the interpretation of KRAUSE's (1993) results, and potentially our own results as well. It would also underline a need for better protocols to study the effect of hunger on shoal choice.

In the case of shoalmate body size, we predicted that well-fed shiners would prefer to associate with conspecifics with size matching their own (as in RANTA et al. 1992a,b; KRAUSE & GODIN 1994), because predators will often concentrate on a group member the size of which differs from the others (the 'oddity effect'; LANDEAU & TERBORGH 1986; THEODORAKIS 1989), but that hungry shiners would tend to associate more with smaller fish, because smaller fish provide less competition for food (COATES 1980; RANTA & LINDSTROM 1990; KRAUSE 1994). In other words, hungry fish would be willing to risk the oddity effect in order to benefit from a lesser competition for food. The effect of hunger on the willingness to risk the oddity effect has not been studied before.

Our choice of variables (hunger in the choosing fish, shoal size and shoalmate body size in the group being chosen) was meant to test the idea that there is a trade-off between foraging and antipredator benefits in the decision of an individual fish to join one shoal over another. We predicted that satiated fish would attach less importance to foraging benefits and would prefer to associate with shoals having characteristics that were more consistent with protection from predators (i.e. shoals that were larger and made up of individuals with body size matching that of the choosing fish); conversely, we predicted that hungry fish would choose shoals that offered less competition for food (i.e. fewer and smaller shoalmates) even though such shoals offered less protection against predators.

Methods

Protocols

Several hundred golden shiners were minnow-trapped in Folly Lake, 12 km south of Moncton, New Brunswick, during the summers of 1995 and 1996. They were separated according to total length (small: 4.7–7.0 cm; large: 8.6–10.2 cm) and left in large aquaria (140 × 30 × 45 cm) for at least 2 wk before the start of experimentation. Water temperature was 17 ± 2 °C. Lighting came from windows in the room. Fish were given a maintenance diet of commercial food flakes at regular intervals throughout the day.

Tests took place in a separate windowless room lit by overhead fluorescent lights. A timer turned the lights on and off at the approximate times of sunrise and sunset for that time of the year. The experimental set-up consisted of three aquaria (50 × 25 × 30 cm) arranged end-to-end. The bottom of each aquarium was covered by 1–2 cm of gravel. Each aquarium also had an outside-mounted power filter centred on the long side at the back. Behind the middle aquarium was a piece of white cardboard; on it, two vertical lines divided the aquarium in three equal sections. Opaque cardboard screens were also present between the aquaria.

At least 24 h before the beginning of a test, shoals were placed in each end aquarium; single test fish, for their part, were introduced into the middle aquarium 2 h before the test. Test fish were chosen haphazardly from the captive stock. They were either well fed (fed to satiation with flakes 2 h before the test, in a separate aquarium) or hungry (no access to food for the 48 h that preceded the test, also in a separate aquarium). At the beginning of a test, the screens between the aquaria were removed, and a camcorder recorded the movement and position of the test fish for 25 min.

This protocol has been used with minor variations in many previous studies, but always with small aquaria and for relatively short observation periods, as was the case here. The question may arise as to whether the choosing fish perceives the two stimulus shoals as truly separate or simply as two parts of a same shoal, and whether its shoal preference is stable over a period of several hours rather than minutes. We therefore replicated all of our experiments with larger test aquaria (140 × 30 × 45 cm for the middle aquarium and 76 × 30 × 40 cm for the end aquaria) to increase chances that the test fish would perceive the shoals as truly separate. Moreover, these replicated tests lasted 5 h rather than 25 min, with the camcorder recording 5 min of fish behaviour at intervals of 1 h. Hereafter, we refer to the two different protocols by mentioning the aquarium size (small or large) although one must remember that there was also a difference in the duration of the observation period (shorter in the small aquaria, longer in the large aquaria).

Experiments

Four experiments were conducted (and each one was replicated, as explained above). The first two experiments concerned shoal size: in the first one, test fish were given a choice between a shoal of 10 shiners and a shoal of 3 shiners, whereas in the second one the choice involved 20 vs. 3 shiners. These shoal sizes were the same as those used by KRAUSE (1993). All shoal members were chosen haphazardly from the same size class as the test fish.

The other two experiments concerned shoalmate body size. In one experiment the test fish were large, and in the other experiment they were small. Test fish were given a choice between a shoal of large shiners and a shoal of small shiners. Shoal size was 5 in the protocol with small aquaria, and 11 in the protocol with large aquaria.

For most experiments, 12 well-fed and 12 hungry fish were individually tested (in some cases, respective sample sizes of 10 and 10 were used, see results). Between tests, shoal composition was changed and shoal position alternated between left and right to control for any potential side bias not related to the shoals on that side.

Data Analysis

From the videotapes, the amount of time that each test fish spent on the left or right third of its tank was measured, and this was taken as an index of shoal choice. The middle section was considered a 'no-choice' zone. Overall shoal preference was determined through binomial tests against the null hypothesis that half of the total number of test fish would spend more time near one type of shoal, and half near the other type. The actual percentage of time spent near a given type of shoal was compared between satiated and food-deprived fish with t-tests (Statistix 4.1). We also used t-tests to compare the number of times that satiated and food-deprived fish crossed either of the two vertical lines that delimited the sections (our measure of fish mobility). Significance level was set at p = 0.05. Results are reported as mean ± SD, except on figures where SE is used.

All statistical analyses involved data from the 25-min observation period as a whole. Beforehand, we checked whether important changes in shoal preference took place within that period (see KRAUSE 1994 for an example of such changes). In the experiments with small aquaria, we divided the 25-min recording in five successive blocks of 5 min. In the replicates with large aquaria, there were already five blocks of 5 min, one block for each hour. We used Friedman tests (Statistix 4.1) to compare the five blocks among themselves for all 32 combinations of time spent near each shoal by each test group (well fed or hungry) in each experiment and protocol (2 shoals × 2 test groups × 4 experiments × 2 protocols = 32). With six exceptions, we found no significant differences among the five time blocks. Four of the exceptions came from the hungry and the well-fed large fish offered a choice between small and large shoalmates in small aquaria; the other two exceptions came from the well-fed small fish given a choice between small and large shoalmates in large aquaria. In all of these six cases, results indicated a significant strengthening of the initial preference shown by the test fish. Overall, we considered that the preference of the test fish did not reverse and did not abate over time, and we felt justified in using the full 25-min period in the analyses.

Results

10 vs. 3 Fish

In small aquaria, both satiated and hungry fish preferred the larger shoal: for both the satiated and hungry groups, 10 out of 12 shiners spent more time near the shoal of 10 conspecifics (p = 0.02). Satiated and hungry fish did not differ significantly in either the time spent near the big shoal (Fig. 1a), time spent near the small shoal (Fig. 1a), or the number of times they crossed either of the two background lines during the test (satiated: 55.1 ± 26.7; food-deprived: 56.6 ± 28.3; t = 0.13, p = 0.89).

In large aquaria, satiated fish had a tendency to again prefer the larger shoal, whereas hungry fish chose both shoals equally: 9 of 12 well-fed fish (p = 0.07) and 6 of 12 hungry fish (p = 0.61) spent more time near the shoal of 10. As in the first protocol, well-fed and food-deprived shiners did not differ significantly in percentage of time spent near the big shoal (Fig. 1b), small shoal (Fig. 1b), or in general activity, although a trend was present for more line crossings in hungry fish (satiated: 19.9 ± 28.1; food-deprived: 42.4 ± 27.5; t = 1.79, p = 0.09).

20 vs. 3 Fish

In small aquaria, well-fed fish significantly preferred the larger shoal, but hungry fish did not: all 12 satiated shiners spent more time near the shoal of 20 (p = 0.0001), but only 8 of 12 hungry fish did so (p = 0.19). As compared with satiated fish, food-deprived individuals spent significantly less time near the shoal of 20 and more time near the shoal

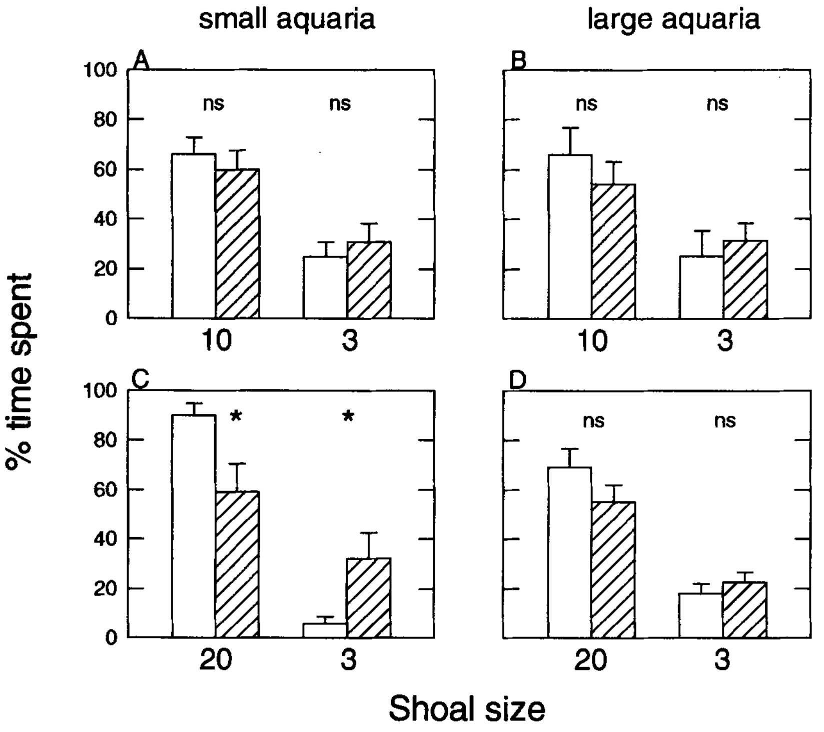

Fig. 1: Percent of time (mean ± SE, n = 10–12) spent near shoals of various sizes by golden shiners that have been either well fed (open bars) or deprived of food for 48 h (hatched bars). These two groups were compared with t-tests (*: $p < 0.05$; ns: $p > 0.05$). See text for differences between the protocol with small aquaria (left panels) and the protocol with large aquaria (right panels)

of 3 (Fig. 1c). Satiated and food-deprived fish did not differ significantly in the number of times they crossed any of the two background lines during the test (satiated: 33.9 ± 30.2; food-deprived: 48.1 ± 31.6; $t = 1.12$, $p = 0.27$).

In large aquaria, both well-fed and hungry fish preferred the larger shoal: all 10 well-fed fish ($p = 0.001$), and 9 of 10 hungry fish ($p = 0.01$), spent more time near the shoal of 20. As compared with the results in small aquaria, well-fed fish spent less time near the larger shoal and more near the smaller one (compare Fig. 1c,d), with the consequence that the difference between well-fed and food-deprived fish became non-significant (Fig. 1d). There was a trend for the hungry fish to be more mobile (82.6 ± 51.9 vs. 42.5 ± 51.5 line crossings) but it was not significant ($t = 1.73$, $p = 0.10$).

Large vs. Small Fish, by a Large Fish

In small aquaria, 11 of the 12 large satiated shiners spent more time near the shoal made up of other large fish than near the shoal of smaller ones ($p = 0.003$). In contrast, 10 of 12 food-deprived shiners reversed this preference and spent more time near the shoal of smaller fish ($p = 0.02$). Hungry large shiners spent significantly less time near the shoal of large fish, and spent significantly more time near the shoal of small fish, than did satiated shiners (Fig. 2a). Satiated and hungry shiners did not differ in their level of activity during the test (satiated: 58.7 ± 24.1 line crossings; food-deprived: 57.3 ± 30.1; $t = 0.12$, $p = 0.90$).

The other protocol with large aquaria gave very similar results (Fig. 2b): 9 of the 10 large satiated shiners preferred the shoal made up of other large individuals ($p = 0.01$), while the same proportion of food-deprived fish preferred the shoal of smaller individuals. Once again, activity levels were similar for both satiated (61.9 ± 15.9) and food-deprived (70.6 ± 16.3) test fish ($t = 1.21$, $p = 0.24$).

Large vs. Small Fish, by a Small Fish

In small aquaria, small satiated shiners unexpectedly showed no consistent preference for any shoal; only 7 out of 12 spent more time near the shoal made up of other small fish ($p = 0.39$). However, a significant 10 of the 12 food-deprived fish did so ($p = 0.02$). In terms of time spent near either shoals, t-tests revealed no difference between well-fed and food-deprived test fish (Fig. 2c). Similarly, there was no significant difference in terms of activity (satiated: 56.1 ± 26.0 line crossings; food-deprived: 47.0 ± 28.5; $t = 0.82$, $p = 0.42$).

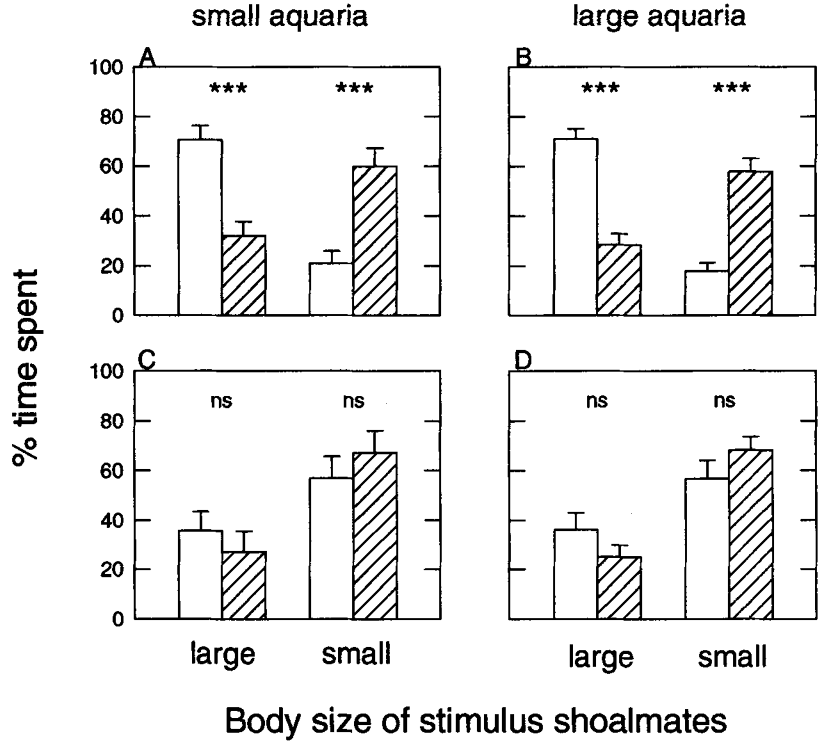

Fig. 2: Percent of time (mean ± SE, $n = 10$–12) spent near shoalmates of various body sizes by golden shiners that have been either well fed (open bars) or deprived of food for 48 h (hatched bars) and that were either large (top panels) or small (bottom panels). Well-fed and food-deprived fish were compared with t-tests (***: $p < 0.001$; ns: $p > 0.05$). See text for differences between the protocol with small aquaria (left panels) and the protocol with large aquaria (right panels)

In large aquaria, both satiated and food-deprived fish spent more time near the shoal made up of other small individuals; 8 of 10 satiated fish ($p = 0.05$) and all 10 hungry fish ($p = 0.001$) did so. The well-fed and hungry groups did not differ in time spent near either shoal (Fig. 2d), nor in activity levels (satiated: 66.9 ± 16.3 line crossings; food-deprived: 65.9 ± 9.5; $t = 0.17$, $p = 0.87$).

Discussion

Comparing Protocols

In terms of the average percentage of time spent near each shoal, the two protocols (small aquaria and short observation time vs. large aquaria and long observation time) yielded similar results, with the sole exception of well-fed fish in the choice between shoals of 3 and 20 (compare the left and right panels within Fig. 1 and within Fig. 2: the only discrepancy between panels is for the open bars at the bottom of Fig. 1). In terms of the proportion of test fish showing a given preference, binomial tests could sometimes detect significant preferences in one protocol but not in the other (although tendencies were always in the right direction; see results for hungry fish in the two experiments on shoal size, and for small well-fed fish in their experiment on shoalmate size).

Overall, the difference in results between protocols is not strong enough to conclude that the distance separating the two stimulus shoals affects the decision of the choosing fish (at least in the range of 50–140 cm, or about 6–20 body lengths). It could be argued that the two shoals in the protocol with small aquaria were perceived by the test fish as parts of a same shoal, given that the distance separating them was well within the diameter of wild shoals. The results would then reflect within-shoal discrimination, a phenomenon that has been reported in other species (PITCHER et al. 1985, 1986; KRAUSE 1994). Such a view would not apply as well to the protocol with large aquaria, however; although the distance separating the two stimulus shoals was also within the diameter of wild shoals, it is unusual to see large (140 cm) empty spaces within such groups (pers. obs.). Such a situation would seem more likely to be the first step in the splitting of a shoal, although shoal splitting is hard to see in free-living golden shiners and has seldom been observed. It would be interesting to determine whether shoal splitting occurs along the line of previous within-shoal discrimination.

The relative similarity of results between the two protocols, as well as the lack of changes over time within each protocol (see last paragraph of Methods), suggest that shoaling preferences are relatively constant within the first 5 h. A review of the literature on shoal preference reveals that choice tests are usually short; our results indicate that, for golden shiners at least, it is not necessary to make such tests last longer (but see KRAUSE 1994 for a different outcome in the chub, *Leuciscus cephalus*).

Hunger and Shoal Size

In the 10 vs. 3 choice, both well-fed and food-deprived fish showed a significant or nearly significant preference for the group of 10, except for food-deprived fish in large aquarium (see binomial tests). In the 20 vs. 3 choice, both well-fed and food-deprived fish also preferred the larger shoal, although in small aquaria this preference was weaker for the food-deprived fish (binomial and t-tests). These results are consistent with those of KRAUSE (1993), who also observed a preference for larger shoals in threespine sticklebacks, but less strongly in hungry individuals.

Decreased preference for the larger shoal might be an artefact of increased mobility by a hungry test fish in search of food: the fish would stop paying attention to the shoals and would simply try to find food within the test tank, bringing his apparent shoal 'preference' closer to random. Three considerations argue against this possibility. Firstly, we detected no statistical difference between the mobility of food-deprived and well-fed test fish. (However, the large variance associated with this particular variable greatly reduced the power of our t-tests. We conducted a post-hoc power analysis (ZAR 1984) and found that, in our situation and for a power level of 90%, the minimum detectable difference between the two groups varied between 19 and 70 line crossings per 25 min depending on the experiment.) Secondly, we witnessed no obvious foraging behaviour in our fish deprived of food for 48 h (in contrast, during preliminary experiments, we observed fish deprived of food for 72 h to actively swim along the bottom with their snout close to the substrate). Thirdly, in the subsequent experiments on shoalmate body size, small hungry shiners did not decrease their preference for small shoalmates as compared with well-fed fish (if anything, their preference increased: Fig. 2c and 2d). This could not have happened if the hungry fish's attention to shoals had diminished because of a more intense search for food.

Decreased preference for the larger shoal seems more likely to reflect an increased sensitivity to the higher food competition posed by a larger or denser group. This would be more acute in very large shoals, and accordingly we found stronger hunger effects in the 20 vs. 3 than in the 10 vs. 3 experiment (see significant t-tests on Fig. 1). The lack of a complete reversal of preference (the shoal of 3 was never significantly chosen) may reflect the still-present influence of predation risk, as well as the fact that very small shoals may provide some foraging disadvantages such as lower rates of food finding (PITCHER et al. 1982). The question then becomes: at what small group size does the disadvantage of low rates of food finding become greater than the disadvantage of food competition in the larger shoal? KRAUSE (1993) found that hungry threespine sticklebacks preferred groups of 10 and 20 over shoals of 3, while VAN HAVRE & FITZGERALD (1988) found that hungry sticklebacks preferred groups of 15 over 45. As compared with 3 or 45, a shoal of 10–20 sticklebacks may represent the best compromise between predation risk, food-finding rate and food competition; very small shoals are disadvantageous because of low rates of food finding and poor protection against predators, while very big shoals are disadvantageous only because of food competition. One would therefore expect well-fed fish to prefer large shoals and hungry fish to prefer intermediate ones.

Hunger and Shoalmate Body Size

When a small fish has a choice, it should join other small fish rather than larger individuals, be it hungry or well fed. Both predation considerations (the oddity effect) and food competition considerations (smaller fish are less competitive) dictate this to be the right choice. This is what we observed, albeit not significantly on a binomial test in the case of the well-fed shiners in small aquaria.

Large shiners, when well fed, also joined shoalmates of size matching their own, as expected. However, when food-deprived they reversed that preference, joining smaller fish instead. This is consistent with the hypothesis that hungry fish recognize the relative competitive ability of shoalmates and prefer to associate with the poorer competitors (see METCALFE & THOMSON 1995 for similar results with dominance status rather than body size). Smaller individuals are likely to be poorer competitors (COATES 1980; RANTA & LINDSTROM 1990; KRAUSE 1994) because they cannot resist displacement and they ingest food more slowly. The latter is more likely to be the true reason for a scramble competitor like the golden shiner.

If the choosing fish is hungry enough, the benefits accrued from reduced food competition may overwhelm the risk of predation due to the oddity effect. Apparently inconsistent with this view is the observation that, in chub, large individuals actually feed less when they are alone among smaller fish, presumably because they feel the need to be more vigilant (KRAUSE 1994). In that experiment, however, fish had been deprived of food for only 6–8 h, a level of starvation that may have been too low to make food competition more important than vigilance.

Hunger and Predation Risk

Foraging often entails increased exposure to predators. Hungry animals should be more willing to forage and therefore more willing to risk predation (MCNAMARA & HOUSTON 1986). This is indeed the case: hungry fish form shoals that are smaller (RICHARDSON 1994), less dense (ROBINSON & PITCHER 1989; ROBINSON 1995), and less cohesive (MORGAN 1988a), attributes that favour foraging but make the shoal more vulnerable to predation. Hungry fish also spend more time at the frontal periphery of the shoal (KRAUSE et al. 1992), where they can find food first but are also more exposed. Hungry fish respond less to alarm pheromones (SMITH 1981; BROWN & SMITH 1996), expose themselves more (DILL & FRASER 1984), inspect predators more (GODIN & CROSSMAN 1994) and resume feeding more quickly after exposure to a predator (MORGAN 1988b; GOTCEITAS & GODIN 1991), as do parasitized and presumably energy-stressed sticklebacks (GILES 1983, 1987; MILINSKI 1985; GODIN & SPROUL 1988). Hungry fish may also prefer habitats that are richer in food but also more risky for predation (MAGNHAGEN 1988). (See also WELLBORN & ROBINSON 1987; MCKILLUP & MCKILLUP 1994; KOIVULA et al. 1995; LIMA 1995; SKUTELSKY 1996; and WEARY et al. 1996 for examples in animals other than fish.) To this list we can now add that hungry fish are more willing to risk the oddity effect: they will join smaller individuals to enjoy a competitive edge in foraging, even though they may thereby become more conspicuous to predators.

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