



Can a minority of informed leaders determine the foraging movements of a fish shoal?

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There is no information on whether the daily foraging movements of fish shoals are the result of chance, the collective will of all shoalmates, or the leadership of a few individuals. This study tested the latter possibility. Shoals of 12 golden shiners, *Notemigonus crysoleucas*, were trained to expect food around midday in one of the brightly lit corners of their tank. They displayed daily food-anticipatory activity by leaving the shady area of their tank and spending more and more time in the food corner up to the normal time of feeding. Past this normal time they remained in the shade, even on test days when no food was delivered. Most of these experienced individuals were then replaced by naïve ones. The resulting ratio of experienced:naïve fish could be 5:7, 3:9 or 1:11. On their own, naïve individuals would normally spend the whole day in the shade, but in all tests the experienced individual(s) were able to entrain these more numerous naïve fish out of the shade and into the brightly lit food corner at the right time of day. Entrainment was stronger in the 5:7 than in the 1:11 experiment. The test shoals never split up and were always led by the same fish, presumably the experienced individuals. These results indicate that in a strongly gregarious species, such as the golden shiner, a minority of informed individuals can lead a shoal to food, either through social facilitation of foraging movements or by eliciting following behaviour.

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When a fish shoal is moving, what determines the direction of its movement? Randomness is of course a possibility, but a more interesting alternative is that at least some of the individuals within the shoal know where they are going. This gives rise to a new question: do most of the group members know where they are going, or are shoal movements controlled mostly by a few leaders?

In the case of migrations that recur on a regular basis (daily or seasonal), it seems likely that most group members know where they are going. Most shoalmates should have had the chance to learn the migratory route by following experienced individuals on previous trips. Although there may be leaders in the sense that the same individuals are always found at the front (Mazeroll & Montgomery 1995), the overall movement of the whole group is not necessarily determined by them. If such leaders were experimentally removed, the rest of the group would still be able to find its way to the correct destination. For example, Helfman & Schultz (1984) showed that transplanted grunts, *Haemulon flavolineatum*, could, in just a day or two, learn the daily migration route used by resident fish between their foraging and resting

sites. When all residents were removed, the transplants were able to migrate on their own along the new route, provided they had had a chance to migrate at least twice alongside the residents.

The question becomes more problematic when one considers the excursions of foraging groups. The spatio-temporal pattern of food availability can change from week to week, if not from day to day, and therefore memorizing a previous route or destination is profitable only for a limited time. The composition of foraging groups is often fluid (e.g. Helfman 1984), which means that some group members may know about the current location and temporal availability of food while others may not. If a majority of the group members are equally well informed, then it seems likely that the whole group could go to the right place at the right time without a need for particular leaders. The few uninformed individuals could simply tag along (Hunter & Wisby 1964; Kanayama 1968; Sugita 1980; all in the context of avoidance response) and eventually learn the route themselves (Laland & Williams 1997). But what if only a small minority of the group members are well informed about the current location of food, as may happen when a group moves into new surroundings and is joined by a few informed locals, or when a single group member learns about food location while on a lone trip and then

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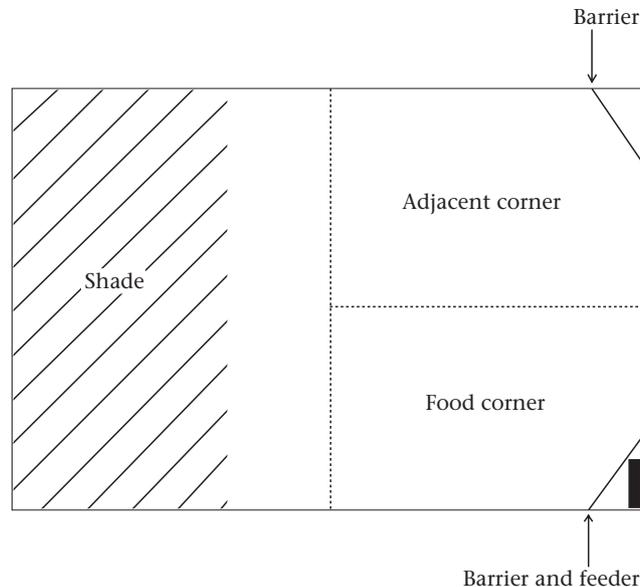


Figure 1. Overhead view of the experimental tank. The dotted lines are imaginary and delineate two areas called 'corners', only one of which received food. Two filter intakes (not shown) were located in the shade and one filter output (not shown) was located dead centre in the tank.

rejoins the group? Could the few lead the many to food?

The present study addressed this question in a species that is strongly gregarious, the golden shiner, *Notemigonus crysoleucas*. This fish forms shoals of 8–250 individuals (Krause et al. 1996) and roams widely within lakes (Scott & Crossman 1973; Hall et al. 1979). In the laboratory, golden shiners can learn to visit a specific corner of their tank at a specific time of day to obtain food (Reebs 1996; Reebs & Gallant 1997), an ability I exploited in this study. I combined a small number of trained shiners with a greater number of untrained and shy fish to determine whether the informed individuals could lead the others out of a refuge area and into the food corner at the appropriate time of day. Either the few informed fish would succeed in leading the whole shoal to the food site or the greater number of shy fish would remain in the shelter and would therefore prevent the trained fish from seeking food. Note that both of these alternatives assume that the shoal could not split up, and therefore the question considered here can only concern strongly gregarious species.

METHODS

Golden shiners, total length 6.0–10.2 cm, were captured with minnow traps in Folly Lake, 12 km south of Moncton, New Brunswick, Canada. Their sex could not be determined. All fish were brought to the laboratory and placed into several 190-litre aquaria. Water temperature was $16 \pm 2^\circ\text{C}$. Light came only from windows in the room and the photoperiod was therefore natural: daylight time varied from 0527–2115 to 0700–1925 hours (local Daylight Saving Time), depending on the season. Fish were fed commercial food flakes, which were dropped at the surface by automatic feeders, five times a

day. All fish were given a minimum of 2 weeks to habituate to these conditions before being used in experiments.

Experiments took place in a large rectangular tank (1.2×1.8 m, or approximately 15×23 fish lengths, with water 8 cm deep). Water temperature and photoperiod were the same as in the holding aquaria. Because of the tank's location close to windows, one end of it was in the shade while the rest was more fully illuminated (Fig. 1). In one of the corners opposite this shady area, small, white pebbles, 5 mm in diameter, were scattered on the bottom. In the other corner, dark blue pebbles twice as big as the white ones were present. The fish could use these pebbles for orientation and corner discrimination. They could also see the ceiling and upper walls of the room above the tank (the walls of the tank itself were opaque).

At the end of the day that preceded the start of an experiment, 12 shiners matched for size were placed inside the tank. The next day, with a camera hanging from the ceiling and connected to a remote tape recorder, I videotaped the movements of the shoal from dawn to dusk. No food was delivered on that day. I expected that the shoal (which I call all-naïve) would spend the whole day in the shady area of the tank. Having never been in this large tank before, the fish were probably shy, and wary fish often seek shade as a refuge (Helfman 1981; McCartt et al. 1997).

Starting the next day, commercial flakes were delivered twice around midday (1230 and 1330 hours) in one of the corners opposite the shady area (Fig. 1). The food was dropped by an automatic feeder which the fish could not see unless they were directly below it. Once on the water, the floating flakes were restricted to a small area in the corner by an opaque Plexiglas barrier at the surface. To reach the food, the fish had to swim to the corner,

and go beyond the barrier (only 2 cm of which jutted below the surface). A few flakes did sink to the bottom and originally these may have alerted the fish to the arrival of food.

After 10 days of such feedings, the food was withheld and the movement of the shoal was videotaped from dawn to dusk. I expected that the shoal (which I now call all-experienced) would have learned about the spatio-temporal availability of food and that it would anticipate food arrival by paying an increasing number of visits to the food corner, or spending an increasing percentage of time there, up to about midday. After midday, the shoal would stop visiting the food corner even though no food had been obtained. A few other fish species are known to increase activity up to the normal time of food delivery and to decrease activity thereafter, even when food is withheld, a phenomenon that is essentially similar to the increased number of food corner visits I expected here (for examples of food-anticipatory activity and internal representation of feeding time in fish, see Davis & Bardach 1965; Spieler & Noeske 1984; Naruse & Oishi 1994; Sánchez-Vásquez et al. 1995, 1997; for a review in other animals, see Mistleberger 1994).

During the next 3 days, the shoal received food around midday again, a reinforcement designed to counter the previous day's negative experience of no food delivery. At the end of the last day, 7, 9 or 11 of the 12 shiners were chosen randomly and replaced by an equal number of similarly sized fish that had never been in the tank before. The next day, no food was given, and the movements of the shoal were videotaped from dawn to dusk. According to the number of trained and untrained individuals in the shoal at that point, the experiments and their corresponding shoals were called 5:7, 3:9 or 1:11. For each of these three experiments there were four replicates, each with new fish right from the start.

I viewed the videotapes on fast-forward and noted the percentage of time spent by the shoals in the food corner and in the adjacent (nonfood) corner opposite the shady area (Fig. 1) for each half-hour of the day. The exact times of entry and departure into and from the corners was taken as when half of the shoal had passed the line that delimited the corners. I also counted the number of entries into the food corner, but this variable was strongly correlated with the percentage of time spent in the corner, and for simplicity I do not present data about entries here.

Although data are presented for the whole day, for analysis I concentrated on two distinctive periods: a food period (1200–1400 hours) centred on the two normal midday feeding times (but remember that food was not delivered on test days) and a food-anticipatory period (1000–1200 hours). The main comparison, for either of those periods, was between the all-naïve and the experimental (1:11, 3:9, or 5:7) conditions to determine whether the experimental fish succeeded in entraining the naïve ones. Differences between these two conditions were ultimately so obvious that no statistical tests were required. I also estimated the strength of entrainment by measuring the proportion of food corner use by the experimental group relative to the all-experienced shoal.

To compare the three experimental conditions in terms of strength of entrainment, I used an ANOVA followed by Scheffe's multiple comparison tests (Statistix 3.5).

If experienced individuals were to entrain naïve ones, I expected it would be by leading, that is, swimming at the front of the shoal and being the first ones to enter the food corner. To ascertain this, it would have been ideal to mark the informed individuals. However, to be visible from an overhead position that covered a field of view of 1.2×1.8 m, the mark would have had to be fairly obstrusive (a white bead threaded through the dorsal musculature, for example). As this could have affected the behaviour of the informed individuals and their attractiveness as shoalmates (let alone as leaders), I decided not to mark the fish. Instead, for a 10-min period during which each shoal entered the food corner at least 10 times, I followed each individual on videotape. If informed fish lead from the front, I expected that in the 1:11 experiment, the first fish to enter the food corner would always be the same individual, while the identity of the fish occupying each of the second, third and fourth position would vary from one entry to the next. In the 3:9 experiment, the first three fish to enter would always be the same, while the composition of the next trio to enter would vary from one entry to the next. In the 5:7 experiment, the first five fish to enter would always be the same, while the identity of the next trio to enter would vary.

RESULTS

On the first day, naïve fish spent all of the daytime in the shady area, as expected. At dawn and dusk, when low light levels extended to the whole tank, the fish often swam around the perimeter of the tank, thereby spending some time within the two corners opposite the shady area, but during the day no time was spent within either of these two corners (triangles, Fig. 2).

Also as expected, after 10 days of midday feeding in one corner, the shoal had learned the spatiotemporal pattern of food availability. Up to about midday, they spent an increasing percentage of time in the food corner (squares, Fig. 2). Typically, the fish left the shady area, entered the food corner, stayed there for about 20–30 s and then returned to the shade. They did this with increasing frequency up to about midday. The fish visited only the food corner and almost never the adjacent nonfood corner. The percentage of time spent in that adjacent corner was consistently low (usually less than 5%; although in four replicates where the shoal passed through this part of the tank on its way to the food corner, values reached as much as 15%; data not shown). After the midday feeding time, the percentage of time spent in the food corner decreased, sometimes rapidly, and remained low until dusk (squares, Fig. 2).

During the 5:7 tests, the shoal kept on visiting the food corner (circles, Fig. 2, left panels). The percentage of time spent in the food corner was high up to midday and decreased thereafter. During the food-anticipatory period, food corner use by the four 5:7 groups was 75, 97, 22 and 85% of that by the corresponding all-experienced groups.

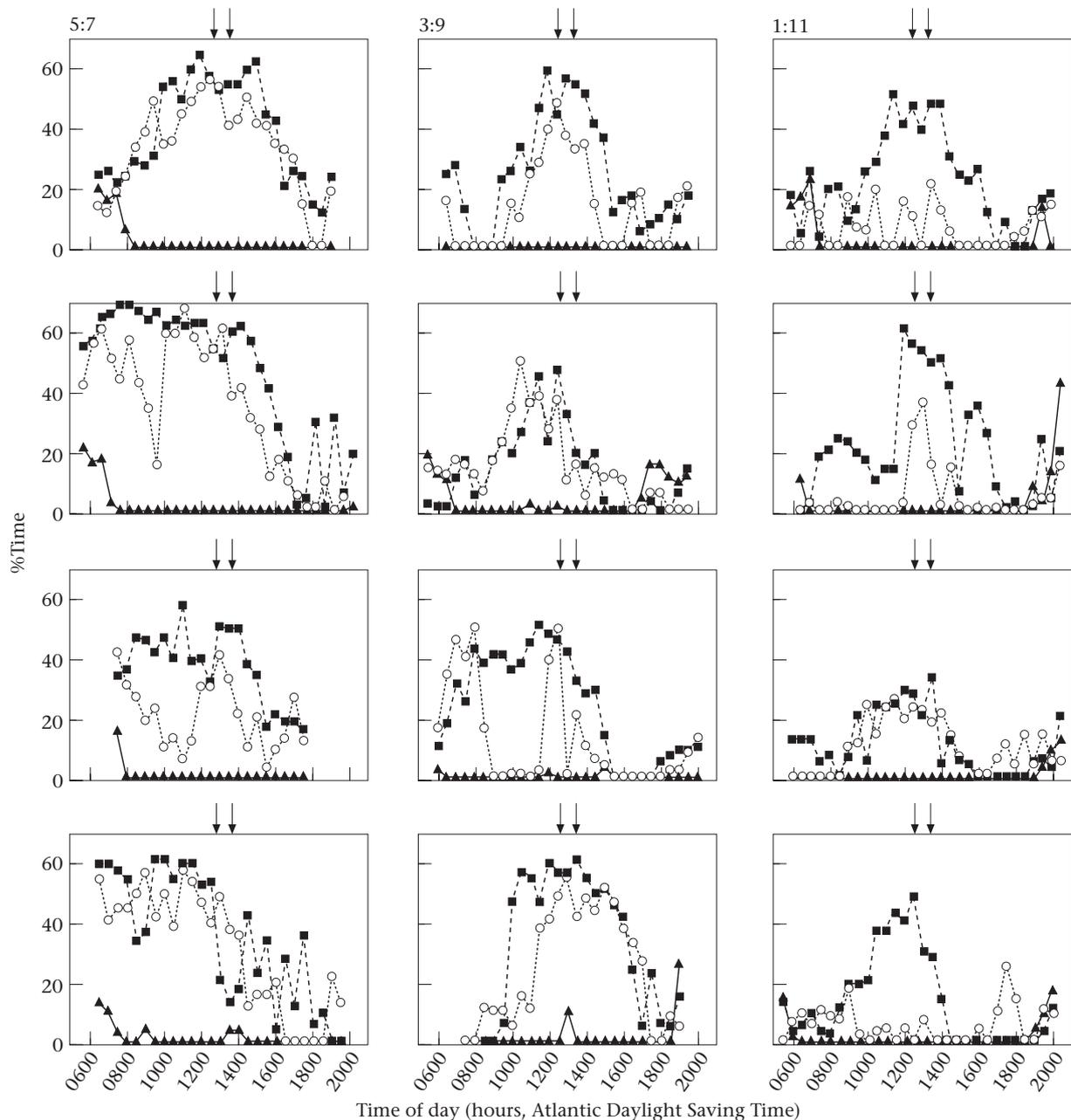


Figure 2. Percentage of time spent in the food corner of a tank by an all-naïve shoal of 12 golden shiners (▲), by the same shoal experienced in being fed twice around midday in the food corner (■), and by that shoal again after some of the experienced fish were replaced by naïve ones (○). Each panel represents an independent replicate where the mixed shoal was made up of either five experienced and seven naïve fish (5:7), three experienced and nine naïve fish (3:9) or one experienced and 11 naïve fish (1:11). Arrows show the normal times of feeding, although food was not delivered on the days when these data were collected.

For the food period, these values were 89, 89, 77 and 123%, respectively. There were only a few visits to the nonfood corner.

In the 3:9 tests, entrainment still took place. The behaviour of the experimental shoal relative to that of the all-experienced shoal was variable during the food-anticipatory period but consistent during the food period (circles, Fig. 2, centre panels). For the food-anticipatory period, food corner use by the four 3:9 groups was 59, 33, 125 and 2% of that by the corresponding all-experienced

groups. For the food period, these values were 60, 80, 74 and 66%. There were only a few visits to the nonfood corner.

During the tests when the shoal contained only one experienced individual and 11 naïve ones (1:11), the results were variable (circles, Fig. 2, right panels). Two shoals left the shade and entered the food corner before the normal time of feeding, but they did so rather infrequently. One shoal visited the food corner a lot more, and in fact showed the same behaviour as the

all-experienced shoal (which, however, had shown the lowest percentage of time spent in the food corner of all all-experienced shoals in this study). The last shoal displayed a short midday peak of visits to the food corner, at levels that were high but nevertheless lower than for the all-experienced shoal. For the food-anticipatory period, food corner use by the four 1:11 groups was 19, 7, 114 and 0% of that by the corresponding all-experienced groups. For the food period, these values were 28, 9, 75 and 38%. There were no visits to the nonfood corner.

One-way ANOVAs between the 5:7, 3:9 and 1:11 groups failed to detect a difference in the strength of entrainment (food corner use relative to the all-experienced shoal) during the food-anticipatory period ($F_{2,9}=0.54$, $P=0.6$). However, there was a difference for the food period ($F_{2,9}=7.91$, $P=0.01$); the 5:7 group showing a stronger entrainment than the 1:11 group (multiple comparison: $P<0.05$).

Visits to the food corner proceeded as follows. During the slow movements of a shoal within the shady area, one or several fish turned towards the food corner and were closely (less than two fish lengths apart) followed by one, then two, then an increasing number of other fish, until the whole shoal made its way out of the shade and into the food corner. In the 1:11 experiment, the first fish to enter the food corner was always the same individual. In contrast, the second, third, or fourth positions were occupied by four to seven different individuals, depending on the position and the replicate. In the 3:9 experiment, depending on the replicate, the first three positions were always occupied by the same three to five individuals (and only the same three fish ever occupied the first two positions). In contrast, six to nine different individuals could be found in the fourth, fifth and sixth places. Finally in the 5:7 experiment, depending on the replicate, the first five positions were always occupied by the same six to seven individuals (and only the same five fish ever occupied the first three positions), whereas the next three positions featured eight different fish.

DISCUSSION

The results show that even a small minority of fish (one individual out of 12) can entrain a whole shoal of naïve and probably shy individuals to food in the right place and at the right time of day. This effect occurred more strongly when the number of experienced fish was greater, as shown by the higher attendance of the food corner during the food period in the 5:7 experiment compared with the 1:11 experiment, and the more variable results of the 1:11 experiment. Nevertheless the entraining effect was substantial even for relatively low numbers of experienced fish: in the 3:9 experiment, food corner use by the experimental groups during the food period was never less than 60% of that shown by the all-experienced shoals.

Is it the absolute or the proportional number of knowledgeable individuals that is most important for entrainment? This question remains to be investigated (but for results in a slightly different paradigm, see Lefebvre & Giraldeau 1994). I have tried to test shoals

made up of three experimental fish and 33 naïve ones (the same ratio as in the 1:11 experiment but the same absolute number of experienced fish as in the 3:9 experiment). Unfortunately the all-naïve control shoals tended to leave the shade spontaneously (their greater number probably made them less shy) and to split up occasionally. The present experimental design would need to be modified before large shoals can be studied, and the nature and feasibility of these modifications remain to be determined.

Over the three experiments, the number of front positions that were consistently occupied by the same individuals in the experimental shoal corresponded roughly to the number of experienced fish. This suggests that these fish entrained the rest of the shoal by leading from the front. Bumann & Krause (1993) have shown that in roach, *Rutilus rutilus*, and three-spined sticklebacks, *Gasterosteus aculeatus*, fish at the front of a shoal tend to steer the whole group. Krause and his coworkers have also shown that hungry individuals tend to lead more often, presumably because this allows them to find food first (Krause et al. 1992, 1998; Krause 1993a), even though it may also expose them more to predators (Bumann et al. 1997). The present study identifies another variable, similar to hunger, that may determine leadership: the motivation to go somewhere at a specific time in order to find food, based on previous experience.

Leaders in the present study entrained shoalmates that would rather have stayed in the safety of the shade, and so the results can be viewed as an example of social facilitation (defined here as an increased tendency by an individual to perform a behaviour after seeing another conspecific do it; see Suboski 1988). There are examples of other behaviours (feeding and vigilance) being socially facilitated or transmitted in fish (Magurran & Higham 1988; Suboski 1988; Ryer & Olla 1991, 1992; Krause 1993b).

On the other hand, perhaps the results could be viewed more profitably as a simple tendency by shy individuals to follow leaders that seem to 'know what they are doing'. Perhaps the followers could even tell that fish in front positions were specifically expecting food (as in Reebbs & Gallant 1997; Lachlan et al. 1998) and that they were worth following for that particular reason. The behaviour of the followers would then be similar to that of colonial birds following neighbours that have displayed signs of successful foraging (Brown 1986; Greene 1987; Rabenold 1987; Waltz 1987), or to that of scroungers in producer-scrounger systems (Barnard & Sibly 1981).

This brings us to the question: what are the possible cues expressed by leaders and perceived by followers that determine who is worth following? In my experiments it seems unlikely that followers were simply motivated by gregariousness; if so, individual decisions by shy fish should have been to stay with the other, more numerous, shy fish rather than follow the few departing leader(s). Some particular behaviour by the leader(s) must have incited the shy fish to follow them. Sudden turns or accelerations are a possibility. Even calls cannot be dismissed; many fishes can vocalize, and examples of

voluntary attraction by calls are known at least from work on birds (Elgar 1986; Brown et al. 1991). Close-up monitoring of leader behaviour will be necessary to shed more light on this question.

There is at least one other example, beside the present study, of a minority of trained fish leading a majority of untrained ones to a food source. Köhler (1976) trained juvenile carp, *Cyprinus carpio*, to swim to a tube in response to an acoustical stimulus (see also Siegmund et al. 1969 cited in Köhler 1976). When a single trained carp was placed with untrained individuals, the stimulus caused the trained fish to swim towards the tube, and at least some of the untrained carp followed. In fact, for shoal sizes up to 10, the whole shoal followed on nearly half of all occasions. For a shoal size of 20, only part of the shoal usually followed. In response to the stimulus, the trained carp repeatedly swam back and forth in front of the shoal, covering short distances in the direction of the feeding station, and this probably constituted an obvious cue for the rest of the shoal. Shiners did not display such obvious behaviour in my study, probably because the stimulus to which they reacted (an internal representation of the daily time at which food was available) was less tangible than the acoustical stimulus used in the classical conditioning paradigm of Köhler (1976). On the other hand, the behaviour of leading shinners in the present study, however subtle and undefined at this point, was probably more natural (in the sense of its possible occurrence in the wild) than that of a conditioned fish reacting to sound.

In a paper on the internal dynamics of fish shoals, Partridge (1981) mentioned unpublished experiments where individuals were conditioned to race to a flashing light in order to obtain food while the rest of a shoal was habituated to that same signal. For both mackerel, *Trachurus symmetricus*, and saithe, *Pollachius virens*, conditioned fish swam to the flashing light when alone but held back when part of a stationary shoal. Details of these preliminary experiments were not given. (What was the proportion of trained and habituated individuals in the shoals? What was the size of the shoal? What was the motivational state of the shoal?) Yet the possibility remains that informed fish may not succeed in entraining whole shoals under certain conditions. Particularly large shoals may represent one such condition (for similar considerations in birds, see Roberts 1997). Although leaders may perform intention movements that suggest leaving in a particular direction, the inertia of large groups may force them to gravitate back to the shoal. Perhaps this is what happens in some fish shoals when 'pseudopods' develop and stretch out from the main body of the group, only to bounce back and reintegrate quickly with the rest of the shoal a few moments later.

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