Who follows whom? Shoaling preferences and social learning of foraging information in guppies

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ABSTRACT

Preferences of fish for different types of shoals may influence the transmission of novel information through them. We investigated the factors influencing the preferences of guppies, *Poecilia reticulata*, for different shoals in order to shed some light on how information transmission occurs. Adult subjects were given a choice between swimming with two diverging shoals of conspecifics that differed with respect to key characteristics. In six choice experiments, subjects discriminated between shoal partners on the basis of: (1) shoal size, subjects preferring a shoal of 10 to a single fish; (2) size of shoaling fish, small fish preferring small conspecifics rather than an equal number of large fish, while large fish showed no preference; (3) local foraging experience of shoaling fish, shoals containing fish that had previously been repeatedly fed in the experimental tank being preferred to shoals with no such experience; and (4) familiarity of shoaling fish, guppies preferring familiar rather than unfamiliar conspecifics. No discrimination on the basis of colour or hunger was observed. In addition, following a shoal to a food site on just three trials allowed guppies to learn a route, or food site, preference. Guppies were considerably more likely to learn to adopt the behaviour shown by members of a shoal of several demonstrators than an alternative behaviour shown by a single conspecific demonstrator. The relationship between preferences for different shoals and the social transmission of information is discussed in the light of these findings. The results suggest that shoaling preferences may strongly influence the social transmission of novel foraging information or feeding preferences through fish populations, and imply that learned information may diffuse through fish populations in a nonrandom, or directed, manner.

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Many species of animal are capable of learning from conspecifics (social learning: Galef 1988a; Lefebvre & Palameta 1988). Field studies suggest that social learning can facilitate the spread of novel behaviour patterns through natural populations (Hinde & Fisher 1951; Goodall 1964; Kawai 1965; Lefebvre 1995; Terkel 1995), while laboratory experiments have explored social-learning processes (Heyes & Dawson 1990; Nicol & Pope 1993; Tomasello et al. 1993; Galef 1996). These investigations have established that much social learning in animals does not require advanced cognitive abilities (Galef 1988a; Whiten & Ham 1992; Heyes 1994); many cases appear to result from very simple processes (Galef 1988a), such as 'local enhancement' (Thorpe 1956),

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where the behaviour of one animal draws the attention of a second animal to a particular stimulus in the local environment. Galef (1988a) has suggested that local enhancement may result from a tendency on the part of naive individuals to approach conspecifics, or alterations they have made in their environment. Shoaling in fish represents such a tendency, and may instigate the transmission of adaptive information between individuals (Laland & Williams 1997).

There is growing evidence that shoaling can enhance foraging success among fish populations, with goldfish, *Carassius* spp., minnows, *Phoxinus phoxinus*, and pollock, *Pollachius* spp., all foraging more efficiently in social groups (Pitcher et al. 1982; Morgan & Colgan 1987; Morgan 1988; Ryer & Olla 1991, 1992). Social learning may be partly responsible for this improvement in performance, if fish acquire up-to-date foraging information from their shoal mates (Pitcher & House 1987; Ryer & Olla 1991, 1992; Laland & Williams 1997). Shoaling mediates social learning in several other aspects of fish behaviour: information about predators is transmitted

through conspecific and heterospecific shoals (Magurran & Higham 1988; Suboski et al. 1990; Ryer & Olla 1991; Krause 1993; Pitcher & Parrish 1993; Mathis et al. 1995); guppies learn a shock avoidance task faster from larger shoals of demonstrators (Sugita 1980); and Helfman & Schultz (1984) and Warner (1988) demonstrated that the routes and mating sites of coral reef fish are 'traditional'.

Theoretical aspects of social learning have been the subject of considerable research, in which the transmission of learned information through populations, and the evolutionary consequences of such processes are modelled (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985, 1988; Laland et al. 1996). Most models treat the diffusion of cultural traits as showing either a deceleratory (e.g. logarithmic) or a sigmoidal (e.g. logistic) pattern over time. A key assumption behind these models is that social interactions occur at random within the population. In general, issues of the effects of social organization, or transmitter–receiver characteristics, on the dynamics of information transmission have been surprisingly understudied. Recently, Coussi-Korbel & Fragaszy (1995) have challenged the notion of random diffusion through a population in discussing the possibility of 'directed social learning', in which transmitted information is restricted to, or directed through, a subset of individuals as a result of various processes influencing social interaction. If swimming with conspecifics allows fish to learn about their local environments, it is pertinent to ask, (1) what factors influence an individual fish's decision to join a particular shoal (including physical or behavioural characteristics of the individual and the shoal members), to establish 'who follows whom'; and (2) whether this results in information spreading through fish shoals in a nonrandom manner.

Many factors may affect an individual fish's decision to shoal and its choice of shoaling partners. These factors include patterns of predation and foraging success, shoal size, and the sex, size and familiarity of the shoaling fish (Theodorakis 1989; Lindström & Ranta 1993; Pitcher & Parrish 1993; Krause 1994; Griffiths & Magurran 1997). In this study we investigated several characteristics that may influence with which conspecifics guppies choose to shoal, and thereby determine from which subset of individuals they are most likely to acquire learned information. Guppies, *Poecilia reticulata*, were chosen because of the strong experimental evidence for social learning, across an array of experimental paradigms, including mate choice (Dugatkin & Godin 1992, 1993), avoidance tasks (Sugita 1980), and foraging-route preferences (Laland & Williams 1997). Guppies typically forage in small, loosely organized shoals, feeding on a variety of food sources, such as benthic algae, aquatic insect larvae and diatoms (Dussault & Kramer 1981; Magurran et al. 1995). They appear to shoal as a response to predation pressure (Seghers 1974), although their shoaling may have other functions (Pitcher & Parrish 1993; Magurran et al. 1995).

Here we present six experiments in which we simulated moving shoals of guppies by placing 'demonstrator' fish inside movable containers, and used these to conduct a shoaling-partner choice test for free-swimming conspecifics. Transparent bottles containing fish have been used successfully to simulate fish shoals in previous experiments that have investigated shoaling and foraging behaviour (Keenleyside 1955; Magurran et al. 1993). Here we modified the technique by moving the bottles apart during the experiment, thereby simulating diverging shoals of guppies. Experimental guppies were given the opportunity to follow demonstrators in one of the two bottles as they were moved apart, and were thereby led to one end of the tank or the other as a consequence of their preferences for characteristics of one of the shoals. The characteristics that we investigated were the size of the shoal, and the mass, colour, hunger level, foraging experience and familiarity of the shoal members. In the case of one of these characteristics (shoal size), we went on to investigate whether foraging information could be learned as a result of this shoaling.

GENERAL METHODS

Subjects and Apparatus

We used 215 guppies in all the experiments, 143 as subjects, with a further 72 as demonstrator fish. All subjects and demonstrators were sexually mature female guppies, purchased from Neil Hardy Aquatics Ltd, London, U.K. As these fish had recently been housed in mixed-sex shoals, we can assume that many of them will have been pregnant. At test, subjects had not been fed for 24 h.

The fish were housed in aquaria of dimensions $60 \times 38 \times 30$ cm for at least a week before being tested, and fed standard tropical fish flaked food once daily. Experiments were conducted in a large aquarium tank (91 cm long × 38 cm deep × 30 cm wide), containing filtered tap water (depth 33 cm), at approximately 25°C. Two white acrylic partitions divided the tank into three regions (Fig. 1), labelled as two 'Goal zones', left and right, and an 'Experimental zone', for exposition. Demonstrators were placed into two, colourless plastic, 2-litre soft drink bottles (diameter: 10 cm; depth of water: 20 cm), creating two simulated shoals. Five demonstrators were placed in each simulated shoal, except in experiment 1 which investigated shoal size. The bottles were suspended from a bamboo pole, fastened along the top of the tank, which allowed us to tow the shoals to the ends of the tank by pulling a string attached to the bottles.

Procedure

First, we placed the demonstrators in the plastic bottles, and left them for 10 min. Then, we placed the subjects in a 500-ml, colourless, plastic cup, which was left in the tank for 5 min, suspended from two strings. During this time, the cup was held still, and next to the two bottles, in the centre of the tank. This was done to allow the guppy to become accustomed to its new surroundings, to allow it to interact (visually) with the members of the simulated shoals, and to give it an opportunity to observe
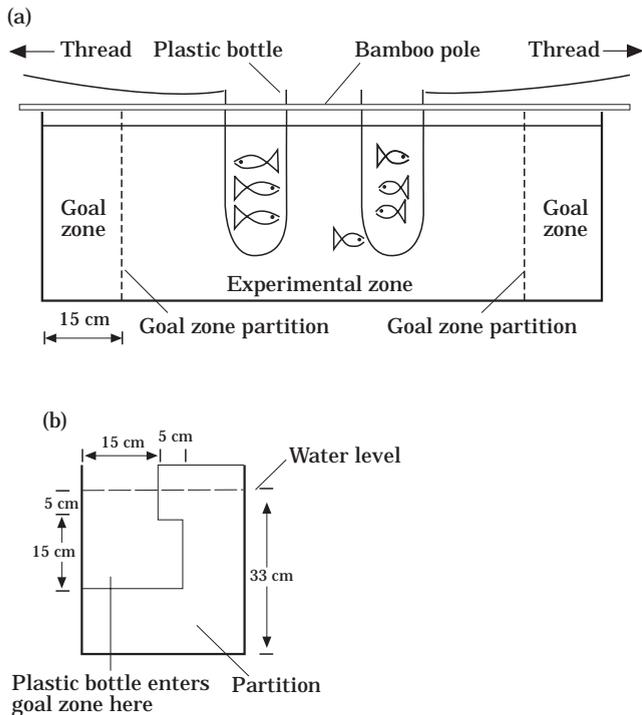
(a)

(b)

Figure 1. The experimental apparatus, illustrating (a) a side view of the experimental tank, and (b) the goal zone partition. The experimental subject had a choice between shoaling with two simulated shoals of fish contained in transparent bottles, which were pulled apart to the two goal zones.

and compare the groups of demonstrators at close range before the shoals separated. After 5 min we released the subject from the cup, and gently pulled the two bottles apart towards either end of the tank. We took care not to bias the subject's choice by moving, or by pointing the cup at either end of the tank. The two bottles were pulled apart such that they reached the end of the tank after approximately 10–15 s. This design feature contrived to mimic the dynamic nature of fish shoals in which subjects regularly have to make rapid decisions about which fish to shoal with, thereby creating a test situation with greater ecological validity than static bottles. Where required (see experiments 1 and 5), subjects or demonstrators were fed with freeze-dried bloodworm (*Chironomus* spp.), after entering the goal zone. The experiment was stopped when the subject entered one of the two goal zones, and we recorded the end chosen. Each shoal was towed with equal frequency to both ends of the tank, controlling for any bias on the part of subjects towards either end. There was no indication from the behaviour of subjects, or demonstrators, that being in the bottles greatly increased stress, or led to unusual behaviour.

EXPERIMENT 1: SHOAL SIZE

Among shoaling fish, members of larger shoals are frequently reported to suffer less predation, and to spend less time in predator detection, than isolated individuals

or fish in small shoals (Morgan 1988; Pitcher & Parrish 1993). In addition, shoaling fish may benefit from enhanced foraging success as a result of the transmission of information about food between shoal members. For example, Pitcher et al. (1982) found that shoal size predicted the speed at which fish discovered food. Such evidence is typically presented as an alternative to the traditional view of group foraging being a trade-off between reduced predation risk and decreased foraging success through competition (see Pitcher & Parrish 1993). It is clear that the cost–benefit balance of predation threat and foraging success will influence an individual fish's decision to join a shoal. In this experiment, we investigated the effect of the number of demonstrators in the plastic bottles on the behaviour of the experimental subjects, with 10 demonstrator fish placed in one bottle, and one demonstrator in the other. Lindström & Ranta (1993) found that male guppies spend more time shoaling with large than small shoals of conspecifics, but as yet there is no information about the preferences of female guppies.

In this experiment we went on to investigate whether any shoal size preference could lead to the social learning of the food site 'used' by the preferred partners. We monitored the ability of guppies to learn a food site preference by repeating the shoaling choice test over three trials, and subsequently testing the subjects to find out if they had acquired a preference for feeding at one end of the tank. In each shoaling trial, subjects were rewarded with food, which was provided in the goal zones, regardless of which group they followed. The three 'observation' trials (with 10 fish in one bottle, and one in the other) were followed by a test, in which the bottles contained shoals that were as far as possible identical (with five fish in each bottle). We reasoned that if, as a consequence of their shoaling preferences, subjects consistently swam to the same end of the tank, they may in the process acquire information about the location of food sites, or the direction to swim in order to find food. Since on the fourth trial, subjects were given a choice between two equivalent shoals, counterbalanced for tank end preferences, any consistent bias for swimming towards a particular end could only reflect any learning on the part of the subjects that had occurred during the three observation trials. We predicted that subjects would swim with the bottle containing the 10 fish, and that they would acquire a preference for the feeding site at the end to which they were led by the shoal.

Methods

We trained subjects for at least 10 days to feed from a red plastic ring, of diameter 2.5 cm, suspended on the water surface, and containing freeze-dried bloodworm. The ring was used to stop food drifting around the tank, and to localize feeding sites.

The subjects were tested as described in the General Methods. There were 10 fish in one bottle, and one fish in the other, the latter being changed for each subject to avoid the experimental results being biased by the particular characteristics of the lone fish. However, the

Table 1. Summary of shoaling preferences observed across the six experiments

Characteristics of shoals	Choice	P
Shoal size: 10 versus 1 demonstrators		
Day 1	18/2	<0.001
Test: 5 versus 5 demonstrators	17/3	0.002
Mass: large versus small demonstrators		
Large subjects	10/6	0.45
Small subjects	3/15	0.008
Colour: bright versus dull demonstrators	12/8	0.5*
Hunger: hungry versus satiated demonstrators	9/11	0.82*
Training: trained versus untrained demonstrators	16/4	0.012
Familiarity: familiar versus unfamiliar demonstrators	12/3	0.036

In each experiment, female guppies were given a choice between two types of shoal. The number of individuals choosing each alternative is shown, together with the two-tailed probability of the finding occurring by chance, computed using a binomial test.
*Power estimate: $0.087 < \beta < 0.195$.

trials continued after the subject had entered one of the goal zones, and was stopped only when it had eaten from one of two red plastic rings, containing a small amount of freeze-dried bloodworm. The feeders were located in the goal zones, and hidden from the experimental zone by the opaque partitions. We recorded the end of the tank from which the subject fed. After the fish had eaten it was caught in a 50-ml cup. Care was taken to avoid stressing the fish during transport between tanks.

Each subject received three such observational trials, with one trial carried out per subject per day, over 3 consecutive days. To counterbalance for tank end preferences, we swapped the directions of the shoals for half of the subjects, but for each subject the end to which the shoal of 10 fish was moved was kept constant over the three observational trials. During this 3-day period, the food provided in the red plastic rings was the only source of food to the subjects. We then tested subjects on a fourth day, using the same procedure but having removed the demonstrators, and replaced them with five similar fish in each bottle. These individuals were chosen such that the two groups matched each other as closely as possible with respect to size and coloration.

Results and Discussion

Female guppies significantly preferred to follow the larger simulated shoals of conspecifics. On the first observation trial, 18 subjects followed the shoal of 10 guppies, while two followed the single demonstrator (Table 1). This preference was also shown on trials 2 and 3, when 17 and 18 subjects, respectively, followed the group of 10 fish, and only three fish changed their preference over the trials; this suggests that the initial preference is fairly stable. Sixteen subjects followed the group of 10 on all three trials and two followed the group twice. Only one subject followed the single demonstrator on all three trials. These results are consistent with those of Lindström & Ranta (1993), who reported a similar preference for larger shoals in male guppies, albeit using a very different methodology.

Significant social learning from the group occurred over the three trials; at test, 17 out of 20 subjects swam to the end to which the group of 10 had been towed in their observation trials (Table 1). This appears to be a result of the preference for following large shoals: out of the 18 subjects who had followed the group of 10 more times than the single demonstrator, 17 went to that end in the test (binomial, one-tailed: $P<0.0001$). The subject that had followed the single demonstrator on all three trials also swam to the end to which the single fish had been towed on its trials. These findings suggest that social learning can occur through shoaling with preferred partners, and that the guppies were more likely to learn from shoals of 10 fish than from individuals, as a consequence of preferring to join shoals of 10 fish than shoals of one fish. In this context, preferential learning from the shoal resulted in a greater tendency on the part of naive fish to learn to adopt the behaviour collectively exhibited by shoal members than to learn the 'nonconformist' behaviour of a single fish.

EXPERIMENT 2: DEMONSTRATOR MASS

The effect of conspecific mass on shoaling behaviour has been investigated in a number of studies (Krause 1994; Krause & Godin 1994). Size-assortative shoaling (the tendency to shoal with conspecifics of a similar size) has been observed, in several species of fish (Theodorakis 1989; Krause 1994; Krause & Godin 1994). Shoaling with fish of similar size is thought to be adaptive since individuals are less likely to stand out in the crowd, and hence to be detected by predators (Pitcher & Parrish 1993). However, other processes may complicate the relationship between joiner and shoal member size. For instance, European minnows prefer to shoal with weaker competitors, even in the absence of cues such as size (Metcalfe & Thomson 1995).

In this experiment, we investigated the effects of demonstrator and subject mass on the shoaling preferences of the subjects. One bottle contained large demonstrators, while the other contained small, but sexually

mature, demonstrators. There were also two groups of subjects, large and small.

Methods

One simulated shoal consisted of five large demonstrators ($\overline{X} \pm SD = 1.6 \pm 0.4$ g), and the other of five small demonstrators (0.2 ± 0.1 g). There were two groups of subjects: 18 small subjects (0.2 ± 0.1 g) and 16 large subjects (0.9 ± 0.2 g). The procedure was as in the General Methods. The fish were weighed after the experiment had been completed.

Results and Discussion

The small subjects significantly preferred small demonstrators: 15 followed the small demonstrators, while three followed the large demonstrators (Table 1). In contrast, the large subjects showed no preference: 10 followed the large demonstrators, while six followed the small demonstrators (Table 1).

These results suggest that small female guppies prefer shoaling partners of their own size. There was a weaker but nonsignificant tendency on the part of larger subjects to follow the large demonstrators. There are at least two plausible explanations for this weaker tendency in larger guppies. The mean mass of the large demonstrators was slightly larger than the mean mass of large subjects, and as a result some of the large subjects might have chosen to assort with the smaller fish. It is also possible, however, that size-assortative shoaling may have greater adaptive advantages for small rather than large fish, if it reduces competition for food, or allows small fish to avoid harassment from larger individuals (Theodorakis 1989; Krause 1994). Adult guppies will eat juvenile individuals, or fry, if given the chance, and guppies in aquaria often bite conspecifics' tails and fins. The apparent lack of preference of larger guppies may reflect a balance between opposing selection pressures, predation risk favouring assortment with equivalent sized conspecifics, but there being foraging advantages to shoaling with smaller individuals. In an analysis of 34 mixed-species shoals in a Canadian lake, Krause et al. (in press) found a relationship between the body length of fish and the degree of size assortedness in the shoal, with the variance in size within shoals correlated with mean body length.

EXPERIMENT 3: COLOUR OF DEMONSTRATORS

Roccanova (1993) proposed an alternative explanation to sexual selection for the evolution of bright coloration in fish: if bright colours tend to attract conspecifics to group with that individual, then since being surrounded by conspecifics reduces predation risk, this process may lead to selection for bright colours. This experiment investigates the effect of the colour of the shoaling fish on the subjects' choice of shoal mates, as well as providing the first empirical test of Roccanova's hypothesis. We constructed two simulated shoals, one consisting of females with bright, red tails, and one consisting of females with very dull, colourless tails. Although females in natural populations of guppies vary little in colour, those from aquatic breeders frequently have bright colours. We exploited this variation to facilitate a more sensitive test of whether the colour of shoal members influences a fish's choice of shoaling partner.

Methods

We selected five demonstrators with especially bright, red tails, and five with especially dull coloration from a group of around 100 females. The difference between the two groups was striking to the human observer, and was almost certainly clear to the guppies, since guppies are known to be able to distinguish between conspecifics (Griffiths & Magurran 1997), and since the tail colour of males is a trait sexually selected by female choice (e.g. Magurran et al. 1995). A sample of 20 adult female subjects of typical dull pink colour was used. The procedure was as in the General Methods.

Results and Discussion

There appeared to be no preference of female guppies to shoal with brightly coloured conspecifics: 12 of the subjects followed the guppies with red tails, while eight followed the group with dull tails (Table 1).

Interpretation of negative findings is difficult in the absence of information about the number of subjects necessary to find an effect that is really there. Consequently, we conducted a power analysis to establish the probability that a type 2 error had been committed in this experiment. The positive results in experiments 1, 2, 5 and 6 were used to estimate the probability of a fish following a preferred target shoal (P). As these probabilities ranged from 0.8 to 0.9, the most conservative estimate of $P=0.8$ was chosen. With a sample of 20 subjects, $P=0.8$ and $\alpha=0.05$, the power of the test is 0.81 for a two-tailed estimate and 0.91 for a one-tailed estimate, giving the probability of a type 2 error (β) between 0.195 and 0.087. β values less than 0.2 are generally regarded as acceptable (Snedecor & Cochran 1989), and hence we conclude that there is reason to believe the negative finding is probably robust. As the distinction between bright and dull shoal members was probably more extreme than that likely to be experienced by individuals in natural populations of guppies, colour is probably not a factor influencing guppy shoal formation. Although we cannot rule out the possibility that colour has a comparatively weak influence, even if it has, its effects are likely to be swamped by other factors that play a more central role in guppy shoal formation. The finding implies, as Paxton & Magurran (1994) suggested, that, at least among guppies, there would be little advantage in terms of predator avoidance of being brightly coloured.

EXPERIMENT 4: DEMONSTRATOR HUNGER

Previous studies have shown that hunger level can generate differences in the shoaling (Morgan 1988) and

exploratory behaviour (Pettersson & Bronmark 1993) of fish. It is possible that hungry and satiated fish present different perceptual stimuli to conspecifics. For example, if hungry fish are more active than satiated conspecifics, they may present a more salient visual stimulus to others. Conversely, considerations of the evolutionary advantages of social learning suggest that it would be adaptive for individuals to follow successful foragers (Laland et al. 1996). This perspective suggests that individuals may prefer to join shoals of satiated fish to shoals of hungry fish. In this experiment, we investigated whether cues indicative of hunger are used by foraging individuals in order to determine which group to follow. We tested this by placing hungry fish in one bottle, and satiated fish in another bottle.

Methods

Hungry demonstrators had not been fed for 24 h at the start of testing, with testing taking approximately 4–6 h. At most, these fish would have been food deprived for 30 h, and this level of food deprivation is not thought to subject the fish to stress (Shubel 1995). The other group of demonstrators had been fed to satiation just before the experiments. There were two differences in the demonstrator groups clearly discernible to us: the satiated group had visibly distended bellies, and appeared less active than the hungry group. We tested 20 subjects (that had not been fed for 24 h) according to the procedure outlined in the General Methods.

Results and Discussion

There was no significant effect of the hunger of the demonstrators on the shoaling preferences of the subjects, with 11 of the subjects following the satiated group of demonstrators and nine following the hungry group (Table 1). A power analysis found the probability of a type 2 error (β) between 0.195 and 0.087, suggesting, once again, that there is reason to believe this negative finding is robust, and the hunger of shoal members is probably not an important factor influencing an individual's decision to join a shoal. However, we cannot rule out the possibility that hunger is a relevant cue within a different range of hunger levels.

One explanation for this finding is that the hunger of others may be an ambiguous cue on which to base any judgment of which shoaling partners are likely to lead to the greatest foraging success. It was clear to us that the hungry demonstrator fish were more active than the satiated demonstrators. However, while hungry fish may be more active, and more highly motivated, they may also be less competent foragers. A satiated fish may be considered an adaptive choice as a potential shoaling partner, because it has recently been a successful forager. However, satiated fish may be less likely to discover further novel food sources, or less well motivated to forage.

EXPERIMENT 5: DEMONSTRATOR EXPERIENCE

Experimental studies have shown that the feeding behaviour of fish often attracts conspecifics (e.g. in goldfish,

Magurran 1984). Moreover, for species in which individuals benefit from being in a group through reduced predation, there may be selection for isolated foragers to behave in ways that attract or recruit conspecifics to a food source. We investigated whether guppies could use the behavioural cues of conspecifics to assess whether to follow demonstrator fish that had been trained to associate being moved to the end of the experimental tank with being fed (henceforth, 'trained' demonstrators), rather than an alternative group of demonstrators that had merely been exposed to the experimental tank for the same length of time, without being fed there (henceforth, 'untrained' demonstrators).

Methods

Both groups of demonstrators were trained for 1 week before the experiment. They were placed in their separate bottles in the experimental tank. We then towed the bottles to each end, as in the experimental procedure outlined in the General Methods. During the training period, when the bottles had reached the ends of the tank, the trained demonstrators were fed a small quantity of freeze-dried bloodworm sprinkled on the surface of the water in the bottle. When this had been consumed, we returned the bottles to the centre of the tank, left them for several minutes, and repeated the process. The trained group of demonstrators was fed repeatedly in this manner, with the bottles swapped over periodically, such that they were fed equally at each end. The untrained demonstrator group was never fed in the experimental tank, but was fed the same quantity of food in their home tank. Each group spent about 20 min in the experimental tank per day, for a week before the experiment. During the experiment, after each trial was completed and the experimental subject had been removed, the trained group were also fed small amounts of freeze-dried bloodworm. We tested 20 subjects. The procedure was as in the General Methods.

Results and Discussion

Subjects significantly preferred the trained demonstrators, with 16 following the trained and four the untrained group (Table 1). The behaviour of the demonstrator fish during the experiment suggested some explanations for this result. During the 5-min period before the trial, when the subject was being allowed to become accustomed to the novel surroundings, and the presence of the demonstrators, there was little obvious difference between the two groups of demonstrators. However, when the bottles began to move towards the end of the tank, the experienced demonstrators became far more active, and typically swam around near the surface of the water, while there was little or no change in the behaviour in the other group of demonstrators. The onset of this active behaviour is probably what attracted the attention of the subjects, and may form the basis of the preference. However, our finding (experiment 4) that guppies show no preference for the overtly more active shoal of

'hungry' fish suggests that other behavioural cues may also be involved. Although previous studies have shown that foraging fish may be attracted to feeding conspecifics, no previous study has demonstrated that behavioural changes in fish that have learned about a food source attracts other individuals some distance from the food source, and some time before the food is eaten.

EXPERIMENT 6: FAMILIARITY

The familiarity of conspecifics is another factor that may influence the dissemination of foraging information through animal populations (Coussi-Korbel & Fragaszy 1995). Griffiths & Magurran (1997) found that guppies recognize familiar shoaling partners, and prefer to shoal with them. They presented subjects with a choice between familiar and unfamiliar guppies in static, perforated bottles, and with the preference measured over a 15-min period. We attempted to replicate their finding, but using the moving bottle techniques described above, with the decision as to which shoal to join having to be made in a matter of seconds, and without access to olfactory information about the shoal.

Methods

Two groups of guppies, one of 20, and the other of five, fish, were selected, and kept separately for 14 days prior to testing (familiarity developed over 12 days in Griffiths & Magurran's study). Five of the former group made up the 'familiar' demonstrator shoal, with the remainder being the experimental subjects. The other group became the 'unfamiliar' demonstrator shoal.

Results and Discussion

There was a significant preference for familiar conspecifics, with 12 of the subjects following the familiar shoal and three following the unfamiliar group (Table 1). Thus Griffiths & Magurran's (1997) finding is clearly robust, even when the fish had to decide quickly with which group to shoal, and when there was no opportunity for olfactory contact between subject and shoal. This raises the possibility that guppies may be more likely to learn from familiar than unfamiliar conspecifics, a point discussed further below.

GENERAL DISCUSSION

Our experiments demonstrate that female guppies use a wide variety of cues to assess potential shoaling partners, including shoal size, mass and familiarity. Similar cues have been shown to affect shoaling behaviour in a variety of fish species (Pitcher & Parrish 1993; Krause 1994). In comparison with other studies, our methods have some unusual features, notably, that after a time to observe both shoals, a decision as to which shoal to follow had to be made relatively rapidly, that the shoals were moving, and that there was no olfactory contact between subject

and shoal. The fact that different methodological approaches repeatedly find evidence for shoaling preferences implies that such preferences are probably robust. Experiment 5 identified another factor that influences shoal formation, namely, behavioural indicators of foraging success. Other factors not investigated in this study may also be of importance. For example, male guppies prefer to shoal with female than male conspecifics (Lindström & Ranta 1993) and social dominance can influence shoaling in salmon, *Salmo salar* (Huntingford et al. 1993). In summary, there is now a substantial body of evidence that shoals are nonrandom assemblages, formed and maintained on the basis of a variety of different shoal member characteristics.

In the light of the empirical evidence that guppies, and shoaling fish in general, prefer particular shoal and shoal member characteristics, we now consider how such preferences may influence the social learning and transmission of information through fish populations. As mentioned in the Introduction, there is considerable evidence that fish are capable of social learning, and experimental studies have demonstrated that simply by shoaling with knowledgeable conspecifics fish can acquire pertinent information about their environment (Laland & Williams 1997). It is clear at the outset that shoaling preferences will create and maintain a structure to fish populations, and by affecting 'who follows whom' such preferences may also influence 'who learns what from whom'.

Coussi-Korbel & Fragaszy (1995), in a review based mainly on field observations of primates, stressed that social organization may restrict the social transmission of information through a population, with social learning dependent on the identity of the 'demonstrator' and 'observer'. They referred to this process as 'directed social learning'. For example, individuals may preferentially learn from demonstrators who are members of the same subgroup, or conspecifics of a similar age, or rank. The differential transmission of particular traits may be biased in a predictable manner by directed social learning. Behaviour patterns should spread quickly to individuals for whom the demonstrators are effective, but relatively slowly to other classes of individuals. In this paper, we have illustrated first, that shoal formation in guppies is strongly dependent on a wide variety of physical and behavioural cues, and second, that this shoaling can mediate the social learning of foraging information. Laland & Williams (1997) also showed that guppies can learn the location of, and route to, a food source by swimming with experienced conspecifics. Experiment 1 also established that the social learning of individual fish is more frequently directed towards groups of demonstrators than a single demonstrator. To the extent that the latter finding can be regarded as an example of directed social learning, our experiments provide clear support for Coussi-Korbel & Fragaszy's position.

Our experimental findings raise the possibility that other factors resulting in shoal-following preferences may also bias the social learning of foraging information, and thereby determine the pattern of diffusion of foraging information through fish populations. For instance, the

findings that guppies prefer to follow familiar individuals, and that small guppies prefer to follow other small guppies, suggest that guppy populations may subdivide, and that, as a result, socially learned information may be restricted to, or directed within, local groups. Size-assortative shoaling may result in more rapid transmission of information between individuals of a given size class, than between size classes. If, as in guppies, size is a function of age, then information may also be directed to within age groups, perhaps inhibiting the flow of information between generations. Such a finding has been discovered in chacma baboons, *Papio ursinus*, where juvenile individuals learn from each other more rapidly than adults learn from them (Cambefort 1981). However, at least in the context of mate choice learning in guppies, younger females can acquire information about potentially suitable mates from older females, indicating that there is a transgenerational flow of information (Dugatkin & Godin 1992, 1993). The preference for following a particular shoal observed in the first trial of experiment 1 was remarkably stable over subsequent trials, perhaps indicating that significant learning of the location of, or route to, the food source may have occurred during the first trial. If rapid acquisition of foraging information is common among shoaling fish, it increases the likelihood that other shoaling preferences may bias what a fish learns. One general implication of this study is that whether a particular behaviour pattern will spread by social learning depends not only on the physiological state of the learner, and the utility of the trait, but also on the frequency of the behaviour pattern in the population, and on other factors that determine grouping patterns. This suggests that social learning researchers might enhance the probability of demonstrating more complex forms of social learning, such as observational learning, emulation, or imitation, by showing greater discrimination in their choice of demonstrating animals, based on the factors that bias aggregation in the species concerned.

The results of experiment 1, that guppies are considerably more likely to adopt the behaviour shown by several members of a shoal of fish than an alternative behaviour shown by a single demonstrator conspecific, is consistent with the observation that guppies learn more effectively from larger groups of demonstrators (Sugita 1980; Laland & Williams 1997). Similar phenomena have been reported in rats, *Rattus norvegicus* (Beck & Galef 1989), and pigeons, *Columba livia* (Lefebvre & Giraldeau 1994). A tendency to shoal with the largest number of fish may generate a positive frequency-dependent transmission of foraging information through fish populations. If individuals tend to do what the majority are doing, this transmission process will result in the most common foraging trait being transmitted more rapidly than expected. The frequency dependence will also mean that a behaviour pattern shown by a small number of individuals would be transmitted at lower rates than otherwise expected, and this may inhibit the diffusion of novel behavioural innovations. This could lead to a diffusion pattern over time resembling a positive exponential curve (Lefebvre & Giraldeau 1994; Laland et al. 1996), rather than the classic sigmoidal pattern anticipated by most theoretical models (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). Any preference to shoal with familiar conspecifics will also tend to inhibit the transmission of novel behaviour patterns between shoals.

The principal finding of experiment 5, that guppies will preferentially follow conspecifics trained to associate moving towards a particular location with being fed, is novel, with exciting ramifications for social learning. The trained demonstrators may reasonably be thought to behave in a manner analogous to a natural group of guppies returning to a known food source, that is, they may be considered analogous to 'successful foragers'. If guppies are able to use simple behavioural cues to judge the potential foraging success of others, and as a result preferentially follow or adopt the behaviour of more successful conspecifics, learning from others would become an extremely effective means of enhancing foraging success. Social learning is often considered to be less adaptive than individual learning in rapidly changing environments, because traits can continue to be transmitted after they are no longer optimal (Boyd & Richerson 1985, 1988). The probability that no-longer-adaptive traits are transmitted would be considerably reduced if observers chose demonstrators on the basis of their current success. The preferential following of successful foragers may also increase the speed with which advantageous behaviour patterns diffuse through a population. Such a preference for following successful foragers has been described in foraging bats, *Nycticeius humeralis* (Wilkinson 1992). Similarly, Giraldeau & Templeton (1991) found that social learning in pigeons was inhibited when the demonstrator foraged unsuccessfully. If the ability of guppies to distinguish between conspecifics anticipating and not anticipating food reliably advances foraging success, then information parasitism or exchange may play a central role in guppy foraging. Guppies forage in a rapidly changing environment, because food sites are ephemeral, and quickly exhausted. The apparent ability to pick out 'successful demonstrators' may be one factor that makes social learning an adaptive strategy for guppies. If information parasitism is occurring, it may be worth investigating whether those individuals anticipating food mask or modify their active behavioural cues when the density of fish is high, and competition for food is intense.

In conclusion, these simple choice experiments on shoaling preferences in guppies have interesting ramifications for understanding social learning and transmission in animals. Our study suggests that, even for simple examples of social learning such as that found in shoaling fish, the pattern of diffusion of novel behavioural variants through a population is likely to be more complex than previously considered, and than presently incorporated into mathematical models (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985).

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