Social learning of foraging sites and escape routes in wild Trinidadian guppies

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We describe two field experiments with wild guppies, *Poecilia reticulata*, in Trinidad that demonstrated that guppies can acquire foraging and predator escape-response information from conspecifics. In the foraging experiment, subjects were presented with two distinctly marked feeders in their home rivers. One feeder contained a conspecific shoal in a transparent container. Guppies preferred to enter the feeder containing this artificial shoal over the other feeder. In a test phase, the artificial shoal was removed and the feeders replaced at the testing site after a 5-min delay. More guppies entered the feeder that had contained the artificial shoal over the other feeder, a difference that can be explained only by the fish learning the characteristics or location of the feeder during the training phase. We suggest that subjects acquired a foraging patch preference through a propensity to approach feeding conspecifics, a local enhancement process. In the predator escape-response experiment, naïve 'observer' guppies could avoid an approaching trawl net by escaping through either a hole to which 'demonstrator' guppies had been trained or through an alternative hole. When the demonstrators were present, the naïve observers escaped more often and more rapidly by the demonstrated route than the alternative route. When the demonstrators were removed, observers maintained a route preference according to the training of their demonstrators, which suggests that the observers had learned an escape route through following or observing their more knowledgeable conspecifics. Thus, both experiments reveal that guppies can socially learn in the wild.

Lefebvre & Palameta (1988) described over 70 field reports of social learning of foraging information, but noted that many of these reports were speculative or anecdotal and provided poor evidence for social learning in the field. Textbook examples of animal social learning, such as the spread of sweet potato washing in Japanese macaques, *Macaca fuscata* (Kawai 1965), have been criticized for not excluding alternative explanations for the spread of the behaviour pattern through the group, such as individual learning or human provisioning (Galef 1992). Lefebvre & Palameta (1988) also observed that

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laboratory studies of social learning, with a few notable exceptions, tend to study tasks unrelated to the types of behaviour reported to be learned in the wild. Hence laboratory experiments are open to the criticism that they lack relevance to the challenges that animals meet in the field. For social learning to be accepted as of real ecological relevance, convincing evidence must be provided that animals in the wild learn from each other. Essential tools in providing such evidence include field experiments (e.g. Lefebvre 1986; Langen 1996; Wilkinson & Boughman 1999), laboratory study of the processes underlying the acquisition of behavioural patterns observed in the wild (e.g. Galef 1980; Terkel 1996) and systematic analysis of between-population variation in behavioural repertoires (e.g. Whiten et al. 1999).

Considerable direct and circumstantial evidence suggests that social learning may enhance the foraging and antipredator behaviour of fish (Brown & Laland 2001). It is well documented that individuals of many fish species, including guppies, are attracted to groups of conspecifics,

particularly feeding conspecifics (Pitcher & Parrish 1993). Individuals may learn the locality of feeding patches from others in this fashion, a social learning process termed local enhancement or area copying (Giraldeau 1997). Enhanced foraging efficiency has been proposed as a possible hypothesis for the evolution of shoaling (Pitcher & Parrish 1993). Moreover, there is evidence that information about novel predators is learned and socially transmitted through shoals of minnows, *Phoxinus phoxinus*, sticklebacks, *Gasterosteus aculeatus*, zebra danios, *Brachydanio rerio*, and salmon, *Salmo salar* (Magurran & Higham 1988; Suboski et al. 1990; Ryer & Olla 1991; Krause 1993; Pitcher & Parrish 1993).

The guppy provides a particularly suitable subject for field studies of social learning. There is good evidence from laboratory experiments that domesticated strains of guppy can learn foraging locations, foraging routes and predator escape routes from conspecifics (Sugita 1980; Laland & Williams 1997, 1998; Lachlan et al. 1998; Reader & Laland 2000; Day et al. 2001; Brown & Laland 2002). However, there is no evidence that fish in the wild learn such information in this manner. Although domestic fancy guppies are convenient for laboratory studies, they are descended from stocks that have been subjected to a great deal of artificial selection (Shubel 1995) and live in very different environments to wild guppies, and so may undergo different behavioural developmental trajectories and have different motivations and behavioural dispositions. Therefore, the extrapolation of laboratory findings to the field and to wild-type guppies may be questionable without appropriate evidence (Dugatkin 1998). Here, we investigated in two experiments whether wild guppies can learn the location of a feeder and an escape route through social processes, to determine whether such processes may be important in guppy foraging and antipredator responses in the field.

The Trinidadian guppy provides some of the best evidence for adaptation to local selection pressures. For example, Endler (1995) listed 45 guppy traits that vary with predation intensity. Guppies from 'high-predation' sites (localities where fish predators dangerous to guppies dwell) typically shoal in larger groups than guppies from 'low-predation' sites (localities where few, less dangerous fish predators live), a relationship that has been documented in both the laboratory and the field, in adults and newborns, and in males and females (Seghers 1974; Magurran & Seghers 1990, 1991; Seghers & Magurran 1995). In contrast, guppies in the Paria River suffer predation from freshwater prawns, but typically swim alone, probably because shoaling provides little defence to this predator (Magurran & Nowak 1991; Magurran et al. 1995). Surprisingly, guppies from a high-predation site on the Oropuche drainage are not strong shoalers, compared with guppies from high-predation sites in the better-studied Caroni drainage basin (Seghers & Magurran 1995). Since such variation between sites could affect learning processes (see General Discussion), we conducted tests at a variety of sites to ensure that our findings were not restricted to a particular predation regime or geographical area.

EXPERIMENT 1: SOCIAL LEARNING OF FORAGING INFORMATION

Methods

Overview

We assessed the performance of wild guppies in a novel foraging task by placing the experimental apparatus into their home rivers. The foraging apparatus consisted of two visually distinct feeders, each of which contained a novel, protein-rich food. Each trial consisted of a training and a test phase. In the training phase, six guppies captured near the testing site were placed within a transparent container in one of the two feeders to form an 'artificial shoal'. These fish could also access the food. The number of additional guppies within each feeder was measured over 5 min. We predicted that guppies would be attracted to feeding conspecifics and so preferentially feed at that feeder. The test phase, conducted after a delay to allow the subjects to disperse from the feeders, was identical to the training phase except that no artificial shoal was present. We predicted that guppies would learn the location of the feeder containing the artificial shoal in the training phase, and would return to this feeder in the test phase. We carried out 34 trials in Trinidad over two field seasons, in March 1999 and February–March 2000.

Field sites

The 1999 trials ($N=12$) were conducted over 2 days, between 1000 and 1600 hours, in the Naranjo tributary of the Upper Aripo (grid reference PS 936 809). The 2000 trials were conducted at seven field sites over 8 days: Upper Aripo (PS 936 809, $N=4$ trials), Middle Aripo (PS 937 797, $N=1$ trial), Upper Tacarigua (PS 798 842, $N=4$ trials), Guanapo (PS 905 805, $N=2$ trials), a tributary of the Paria (PS 891 883, $N=4$ trials; PS 898 882, $N=2$ trials), Quare (PS 974 815, $N=4$ trials) and Turure (PS 005 810, $N=1$ trial). The field sites included rivers of the Caroni drainage basin (Aripo, Guanapo, Tacarigua) and the Oropuche drainage basin (Turure, Quare; Magurran et al. 1993; Seghers & Magurran 1995; Houde 1997).

The field sites were classified as 'high-predation' (Upper Tacarigua, Quare, Guanapo, Middle Aripo; $N=11$ total trials), 'low-predation' (Upper Aripo, Turure; $N=17$ trials) or 'prawn predation' (Paria; $N=6$ trials) according to Magurran & Seghers (1990, 1991, 1994), Magurran et al. (1993) and Houde (1997). Reznick et al. (1996) characterized Paria sites as 'low-predation'. High-predation sites contain dangerous fish predators such as the cichlid piscivore *Crenicichla alta*, whereas low-predation sites typically contain only the less dangerous *Rivulus hartii*, which attacks mainly juvenile guppies (Seghers 1974; Magurran & Seghers 1990, 1991; Magurran et al. 1993). Low-predation sites are often above barrier waterfalls that prevent the upstream migration of many fish predators. Freshwater *Macrobrachium* prawns hunt primarily at night (although at least one species is diurnal), using olfactory and tactile as well as visual cues, and guppies tend to form very small shoals (usually one individual) where these
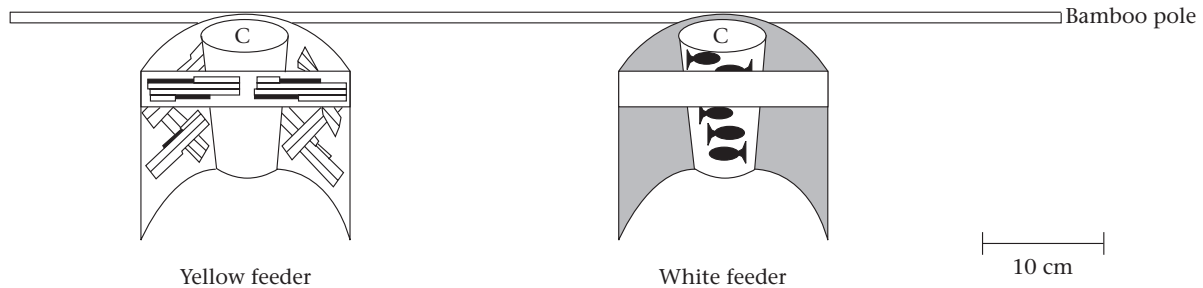
Figure 1. The experimental feeders (three-dimensional view from the front). A mixed-sex group of six guppies was placed into one of two clear plastic 250-ml cups ('C') during the training phase of each trial. During both training and test phases food was sprinkled on the water surface within the feeders, accessible to both the artificial shoal and any fish entering the feeder. The water level was just below the top of the feeders, so that food (and the artificial shoal) could not escape, but subjects could enter and leave through the open front or underside of the feeder.

predators are present (Magurran & Seghers 1990, 1991). We also made a personal visual assessment of the predators present, which matched that of the more formal surveys cited above in all cases. Most of the sites were fairly shallow (ca. 20 cm deep) clear tributaries, consisting of slow-flowing pools linked by regions of faster flow.

Subjects and apparatus

At least 402 subjects were attracted to the feeders. Six adult guppies, three of each sex, were caught using dip nets from a region several metres away from the testing site to serve as an artificial shoal. These fish were chosen to be a range of sizes. At the end of each day of testing, these fish were released at their site of capture.

The foraging apparatus was two visually distinct feeders, each of which contained an excess of food (Fig. 1). The feeders were constructed of white, opaque PVC. To aid visual discriminations, one feeder was marked with yellow and green electrical tape (hereafter 'yellow feeder') and the other feeder was left unmarked (hereafter 'white feeder'). Subjects could freely enter and leave the feeders. The artificial shoal was placed into one of the two transparent plastic cups that allowed visual but not olfactory or tactile contact with the surroundings. Equal quantities of freeze-dried bloodworm, *Chironomus* spp., a novel, high-protein, floating food, could be added to each feeder using forceps.

Procedure

Observations were typically carried out from the river bank, a method that did not seem to disturb the fish and that had previously been used successfully in observations of shoaling tendency (e.g. Seghers & Magurran 1995). Occasionally it was necessary to take observations while standing in the river. The location of the artificial shoal during the training phase was counterbalanced, alternating between the feeders for subsequent trials, with an equal number of trials conducted with the artificial shoal in the white and yellow feeders at each site. To ensure that one feeder was not always upstream of the other, trials were conducted from both sides of the river. The researcher stood equidistant from the two feeders to avoid imposing a side bias. We carried out tests on

separate, independent groups of guppies by conducting each trial in a different pool or, when testing in the open river, by conducting tests at a distance from one another. Guppies prefer relatively still pools and the edges of rivers, with movement of guppies between pools unlikely during the time course of the experiments (Magurran et al. 1995; Houde 1997).

At the beginning of the training phase, the apparatus was placed into the water, typically in a region of slow-flowing water at the river edge, so that the apparatus could rest on the river bed or be supported by the river bank. An excess of freeze-dried bloodworm was added to both feeders. The bloodworm was sprinkled over the entire water surface enclosed in the feeder, so that the fish of the artificial shoal were also able to access the food. The number of fish in each feeder was noted every 15 s for 5 min. If more than 20 fish entered the feeder, we capped the datum for that 15-s period at 20, because we decided that it was not possible to count more than 20 fish accurately. It was not possible to identify, track, age or sex individual fish. At the end of the training phase the entire apparatus was removed from the water.

The test phase began after a 5-min delay, during which time any fish attracted to the feeding sites had dispersed. In one case, the fish did not disperse during this interval, so the test phase was delayed for a further 5 min. The test phase was similar to the training phase, with the apparatus being placed in the river in the same location and an excess of bloodworm again added to both feeders, but no artificial shoal was present. The guppies that made up the artificial shoal were housed in a 500-ml plastic beaker on the river bank during this period. The number of fish in each feeder was noted every 15 s for 5 min, and the test phase ended with the removal of the apparatus from the river. The test phase of one trial was abandoned after only one fish located the feeder during the training phase. Statistics were based upon the mean number of fish present in each feeder over the entire 5-min trial, and all statistical tests described are two tailed. Paired *t* tests were used to pair the data from the two feeders in each trial with one another and compare the number of fish present in each. Where appropriate, we conducted Kolmogorov–Smirnov tests to ensure that the data met the assumptions of parametric analyses.
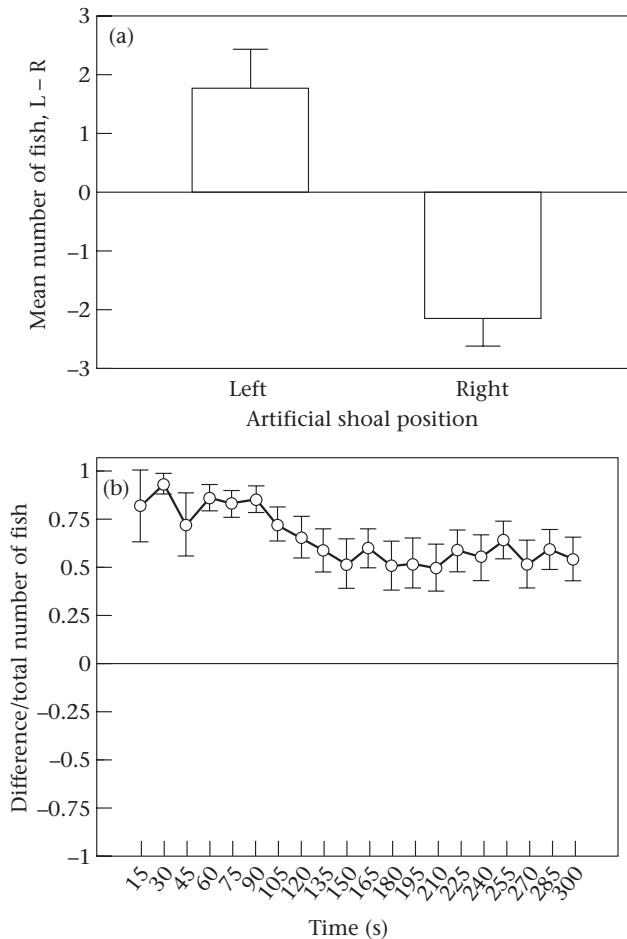
Figure 2. Training phase of the foraging experiment, with an artificial shoal within either the left or right feeder. (a) Mean±SE difference in the number of guppies within the left and right feeders, averaged over 5 min. (b) Mean±SE proportion of guppies within the feeder with the artificial shoal compared with the alternative feeder over the 5-min training phase, calculated by dividing the difference (number of fish in feeder with shoal−number in alternative feeder) by the total number of fish in the two feeders. This provided a measure that ranged from 1.0 (all fish in feeder with artificial shoal) to −1.0 (all fish in alternative feeder).

Results

Training phase

Fish entered the feeder containing the artificial shoal on 33 of the 34 trials, but they entered the feeder with no artificial shoal on only 19 of 34 trials. On 30 of the 34 trials, more guppies entered the feeder containing the artificial shoal than the alternative feeder, on significantly more trials than would be expected by chance (chi-square test: $\chi_1^2=19.88$, $P<0.005$). The mean number of fish per reading in the feeder that contained the artificial shoal was significantly greater than the mean number of fish in the feeder with no artificial shoal (paired t test: $t_{33}=5.25$, $P<0.0001$; Fig. 2). That is, significantly more fish entered the feeder with the artificial shoal. Members of the artificial shoal and guppies entering the feeders fed during the training phase.
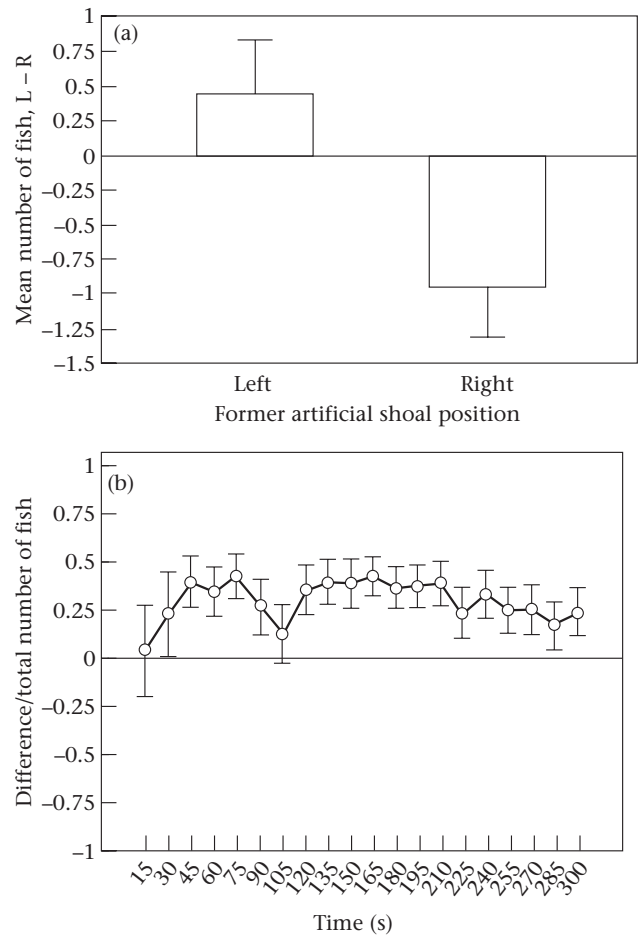

Figure 3. Test phase of the foraging experiment, with no artificial shoal in either feeder. (a) Mean±SE difference in the number of guppies within the left and right feeders, averaged over 5 min. (b) Mean±SE proportion of guppies within the feeder with the artificial shoal compared with the alternative feeder over the 5-min training phase (1.0: all subjects in the feeder with artificial shoal; −1.0: all subjects in the alternative feeder). See Fig. 2 for additional notes.

Test phase

During the test phase, fish entered the feeder that had formerly contained the artificial shoal on 32 of 33 trials, and entered the feeder that had formerly contained no artificial shoal on 25 of the 33 trials. On 21 of the 33 trials, more guppies entered the feeder that had contained the artificial shoal than the alternative feeder on more trials than would be expected by chance, although not significantly so (chi-square test: $\chi_1^2=3.13$, $P=0.077$). The mean number of fish in the feeder that had contained the artificial shoal was significantly greater than the mean number of fish in the alternative feeder (paired t test: $t_{32}=2.64$, $P<0.02$; Fig. 3). That is, significantly more fish entered the feeder that had contained the artificial shoal. The mean number of fish recorded in the feeder that had contained the artificial shoal was similar on the training and test phases (paired t test: $t_{32}=0.17$, $P>0.1$, power=0.80), but more fish entered the alternative feeder on the test phase than the training phase (paired t test: $t_{32}=3.48$, $P<0.002$). Statistical power was estimated based

on an α of 0.05 and Cohen's (1988) medium effect size (Howell 1997).

A similar qualitative pattern of results was observed for the various sites in the three predation regimes on both the training phase and the test phase. The single exception to this finding was the Quare, where the mean difference between the number of fish in the two feeders was near zero. A quantitative analysis (such as a nested analysis of variance, ANOVA) was not possible given the small samples sizes at each site.

Discussion

The guppies examined in this experiment showed a clear preference for a feeder containing feeding conspecifics (in visual but not olfactory or tactile contact) over a similarly rewarded feeder empty of conspecifics. This result suggests that feeding conspecifics are highly attractive to guppies. During the test phase, conducted after a short interval when the artificially restrained shoal of conspecifics had been removed from the feeder, more guppies entered the feeder that had previously contained this shoal. The most plausible explanation for this result is that the subjects had learned the position or characteristics of the feeder during the training phase, presumably through a process of reinforcement when feeding on the high-protein bloodworm. Hence, our experiments reveal evidence that guppies in the wild can socially learn the location of a food source by approaching feeding conspecifics.

The most appropriate description of this acquisition of a patch preference is probably learning through a process of local or stimulus enhancement. Effectively, the feeding conspecifics may provide a 'tip-off' to the location of food. In high-predation areas, approaching and shoaling with conspecifics is also likely to reduce the risk of predation (Magurran et al. 1995), so individuals may discover the food source as a side-benefit of an antipredatory shoaling response. A third possibility for the local enhancement effect found in the training phase is that males were approaching and courting the females in the artificial shoal (Griffiths & Magurran 1998). Male guppies prefer unfamiliar females and swim greater distances than females, presumably in search of mates (Griffiths 1996; Kelley et al. 1999). It was not possible to determine the proportions of each sex approaching the feeders, but in most cases individuals of both sex were present. It is likely that the local enhancement effect that we describe was a result of some combination of these three processes.

Alternative explanations to social learning are unlikely to account for these results. There can have been no residual olfactory cues left by the artificial shoal, because the shoal was held in a plastic cup that prevented olfactory contact with the outside water. Flow rates were sufficient to wash away any residual food left after the training phase and any accompanying olfactory cues. In any case, both feeders were similarly rewarded, containing approximately equal amounts of food. It is possible that fish on the training phase were responding primarily to food pulled beneath the surface rather than to the artificial shoal itself. However, this stimulus would be available only when conspecifics are present, so learning from such a cue would fit the definition of 'social learning' (i.e. learning that is influenced by observation of, or interaction with, another animal or its products; Heyes 1994). The test phase did not begin until all the subjects had dispersed from the feeding area, so we cannot explain the results in terms of the guppies simply remaining in the area where they had previously fed. The fact that feeders were in close proximity (40 cm) makes the results even more striking, because both feeders would have been easily visible and accessible by the fish. Olfactory cues from the subjects impregnating the plastic feeders are an unlikely explanation for the results, because the counterbalancing procedure would counteract any olfactory differences between the two feeders.

One possible explanation for the magnitude of the observed differences between the numbers of fish in each feeder on the test phase is that local enhancement effects had accentuated these differences. That is, an initial difference in the numbers entering each feeder (because more fish had previously learned the characteristics of one feeder than the other feeder) could have been strengthened by additional fish being attracted to the feeder that contained more subjects. However, the finding that similar numbers of subjects entered the artificial shoal feeder on the training and test phases suggests that such an effect is unlikely to account for our results. In addition, a conservative, nonparametric analysis that disregards the magnitude of the difference in the numbers entering each feeder approached statistical significance. Hence, the conclusion that guppies can learn foraging sites from conspecifics appears robust.

EXPERIMENT 2: SOCIAL LEARNING OF ESCAPE RESPONSES

Methods

Overview

We assessed the social learning of an escape route from an artificial predator by placing subjects into a mesh enclosure in their home rivers. A mesh 'trawl' was dragged through the enclosure towards a partition, and subjects could escape from the trawl by passing through one of two visually distinct holes in the partition. The trawl experiment consisted of three stages. First, 'demonstrators' were trained to escape through one of the coloured escape holes, while the alternative hole was closed. Second, demonstrators and 'observers' (naïve guppies) were placed together in the mesh enclosure. Both holes were opened and the escape route taken by the fish observed. Finally, the demonstrators were removed and the escape latency and route of observers were tested to determine whether they had learned a preference for the hole to which the demonstrators were trained. This experiment was carried out at three of the sites described above, Upper Aripo (low predation), Guanapo (high predation) and Paria (prawn predation), in February–March 2000. We conducted 14 replicates and counterbalanced the colour to which demonstrators were trained at each site.
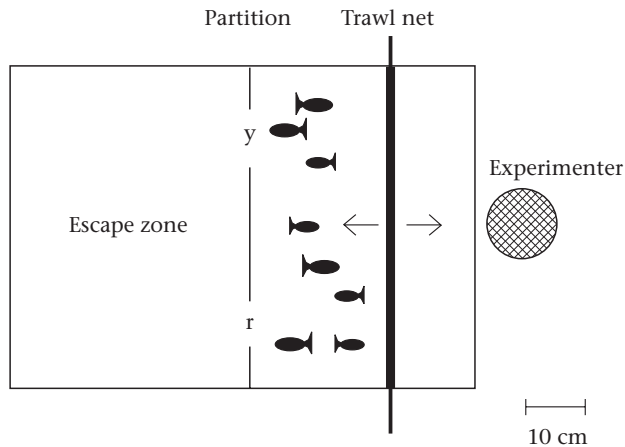
Figure 4. The trawl apparatus, overhead view. The trawl net was moved repeatedly up to within 2–3 cm of the escape holes ('y' and 'r') and back to the starting position by an experimenter (hatched circle) at the downstream end of the mesh box. The escape hole borders were distinguished by homogenous red (hole 'r') or yellow ('y') colour.

Subjects and apparatus

We used 112 guppies, of which 56 acted as demonstrators and 56 as observers. We caught equal numbers of large and small adult guppies using dip nets from a region several metres away from the testing site. There were approximately equal numbers of each sex of both the large and the small fish.

The trawl experiment took place in a mesh box ($88 \times 40 \times 40$ cm; Fig. 4) made of dark green, nylon mesh that allowed water flow. The edges of the mesh box were made of plastic-coated metal rods, to maintain the structure. A white PVC sheet was placed on the base, inside the mesh box, so that the fish could be seen clearly from above. An upright opaque PVC barrier (40×40 cm, 2.5 mm thick) was positioned across the centre of the mesh box. This barrier contained two square escape holes at the base (55 cm^2 each) 15 cm from one another. Each escape hole was bordered by 2 cm of either red or yellow electrical tape to aid visual discrimination by the fish. The square trawl net (39×39 cm) of green plastic mesh was attached to a frame made of plastic-coated metal rod. The metal rods at the top of the square extended on either side to form handles to move the trawl. Brushes were attached to the base and sides of the trawl to prevent fish from escaping around the edges of the trawl.

The mesh box was placed in approximately 30 cm of water near the river bank in an area of weak current and oriented so that the water flowed down the length of the enclosure. Large leaves and stones were placed against the outer sides of the mesh box to minimize side current and thus make it easy for the fish to move freely within the enclosure.

Procedure

Stage 1. Training demonstrators. Four large and four small fish were placed in the mesh enclosure to be trained as demonstrators, whilst the remaining guppies remained

in a holding bucket. The demonstrators were given a 'settling in' period of approximately 12 min. The eight demonstrators were herded into the downstream half of the enclosure by moving an opaque dividing partition down the enclosure. The central barrier containing the escape holes was then erected out of sight of the demonstrators, who were confined between the opaque partition and the trawl net. One of the escape holes in the central barrier was closed off by a piece of PVC sheet placed against the upstream side of the hole, so the fish could still see the coloured borders to both holes during training. The trawl net was 10 cm from the downstream end of the mesh box.

Training took place over eight bouts of 2 min each. Each bout began when the dividing partition was raised, exposing the fish to the escape hole. The trawl net remained stationary for 15 s, allowing the fish to acclimatize and explore the new apparatus. The trawl net was then repeatedly dragged slowly up the enclosure towards the escape holes for 15 s, then back to the starting position for 15 s. The researcher stood at the end of the mesh box to drag the trawl, so as not to impose a visual side bias for the fish. The trawl approached within 2–3 cm of the PVC sheet containing the escape holes to prevent injury of the fish. The time at which fish swam through the escape hole to the upstream half of the enclosure was recorded. If a fish did not escape by the end of the bout, they were awarded a ceiling value of 2 min. This prevented the times of those fish that did escape during the bout from being overrepresented in the mean escape time for the group. Between bouts, the fish were placed back in the downstream half of the mesh box between the dividing partition and the trawl.

Stage 2. Testing demonstrators and observers together. Demonstrators and observers were tested together over five bouts, each lasting 2 min. Because it was difficult to distinguish between fish of the same size, we tested large demonstrators with small observers for a first set of bouts and small demonstrators with large observers for a second set. Demonstrators that were not being used during each set were kept in a holding beaker. During stage 2, both escape holes were open to test whether demonstrators had acquired a preference to escape through the training hole, and whether this affected the observers' choice of escape hole. The remaining procedure was identical to that of the training stage.

Stage 3. Testing observers without demonstrators. We removed the demonstrators and tested the groups of four observers over three bouts of 2 min each, using the same procedure as that of the previous testing stage. The observers were tested in the absence of demonstrators to determine whether they had acquired or learned a preference to escape through the hole used by demonstrators during stage 2.

The colour to which demonstrators were trained was counterbalanced at each site, by repeating the experiment using new demonstrator and observer fish and the alternative escape hole during the demonstrator training stage

($N=8$ groups of observers paired with red-trained demonstrators; $N=6$ observer groups paired with yellow-trained demonstrators). Half of the groups of observers were composed of small fish and half of large fish. All subjects were replaced near their capture site.

Because it was not possible to identify individual fish and the fish within each group that took the same route may not have behaved independently, statistics are based on the mean for each group. Our 'latency' measure was the mean of the subjects' times to enter each hole, and if no fish entered a hole on one bout, the latency score was capped at 120 s. We then took the mean across the bouts within each stage of the experiment. To give a relative preference measure for the two holes, we subtracted the datum for the yellow hole from that for the red hole. Hence a negative latency score indicates that fish entered the red hole more rapidly than the yellow, whereas a negative score for the number of subjects to enter indicates that more fish entered the yellow hole than the red. The use of these difference scores also has the advantage of rendering the data normally distributed (determined by Kolmogorov–Smirnov tests) and allowing parametric analyses to be used. Statistical tests described are two tailed.

Results

Stage 2. Testing demonstrators and observers together

The prior training of the demonstrators had a significant effect on the behaviour of observers. Observers tested with red-trained demonstrators swam more rapidly through the red hole in preference to the yellow hole, compared with observers tested with yellow-trained demonstrators (ANOVA: $F_{1,12}=17.67$, $P<0.005$; Fig. 5a). More observers tested with red-trained demonstrators swam through the red hole in preference to the yellow hole than observers who were tested with yellow-trained demonstrators ($F_{1,12}=17.81$, $P<0.005$; Fig. 5b). The demonstrators showed a preference for the red or yellow hole according to their training (latency to enter: $F_{1,12}=6.24$, $P<0.05$; number entering holes: $F_{1,12}=10.01$, $P<0.01$). There was no significant difference between the mean times of the observers and demonstrators to enter the hole to which demonstrators had been trained (paired t test: $t_{13}=1.78$, $P=0.098$). The body size of observers had no significant effect on task performance (ANOVA: latency: $F_{1,12}=0.00$, NS; number entering holes: $F_{1,12}=0.05$, NS).

Stage 3. Testing observers without demonstrators

The prior training of the demonstrators had a significant effect on the behaviour of observers after the demonstrators had been removed. Observers previously paired with red-trained demonstrators swam more rapidly through the red hole in preference to the yellow hole, compared with observers previously paired with yellow-trained demonstrators (ANOVA: $F_{1,12}=5.37$, $P<0.05$; Fig. 6a). Similarly, more observers who had been previously paired with red-trained demonstrators swam through the red hole in preference to the yellow hole, compared with
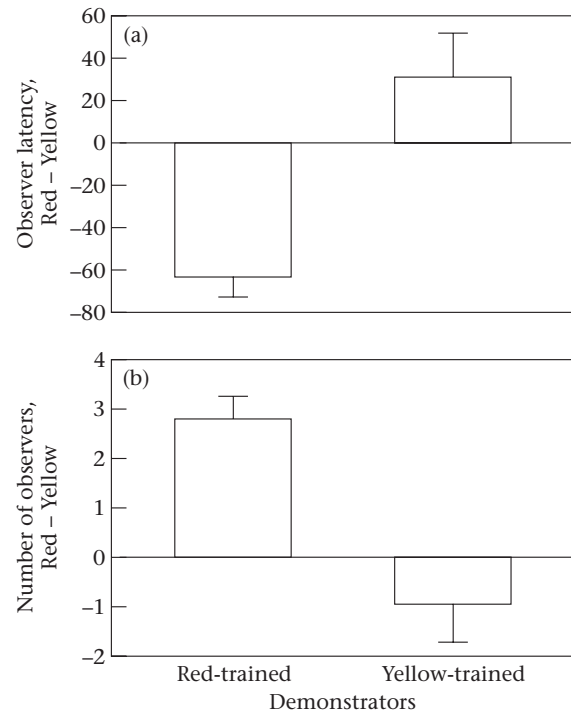

Figure 5. Stage 2 of the trawl-escape experiment, with observers tested with demonstrators trained to one of two escape routes (red and yellow). Only data for observers are shown. (a) Mean±SE difference between the latencies to enter the red and yellow holes. (b) Mean±SE difference in the number of observers to enter the red and yellow holes.

observers who were previously paired with yellow-trained demonstrators, although this difference only approached significance ($F_{1,12}=3.96$, $P=0.07$; Fig. 6b).

From Fig. 6, it is clear there was an overall preference for the red route, but that experience with differently trained demonstrators had a significant effect on route choice. If the behaviour of the demonstrators had no effect on the subsequent behaviour of the observers, similar route preferences should have been observed in the observers regardless of demonstrator training, which was not the case. The body size of observers had no significant effect on task performance (ANOVAs: latency: $F_{1,12}=0.00$, NS; number entering holes: $F_{1,12}=0.03$, NS). We examined the latency scores to determine whether there was a difference between sites. A similar pattern of results was observed at all three sites, with no significant interaction between demonstrator training and field site ($F_{2,8}=1.83$, NS, power=0.2), although statistical power was limited for this analysis. Statistical power was estimated based on the harmonic mean of the sample size for each group, $\alpha=0.05$ and Cohen's (1988) large effect size (Howell 1997).

Discussion

The training of the demonstrators resulted in their swimming faster and more often through the escape hole to which they were trained over the other hole. When
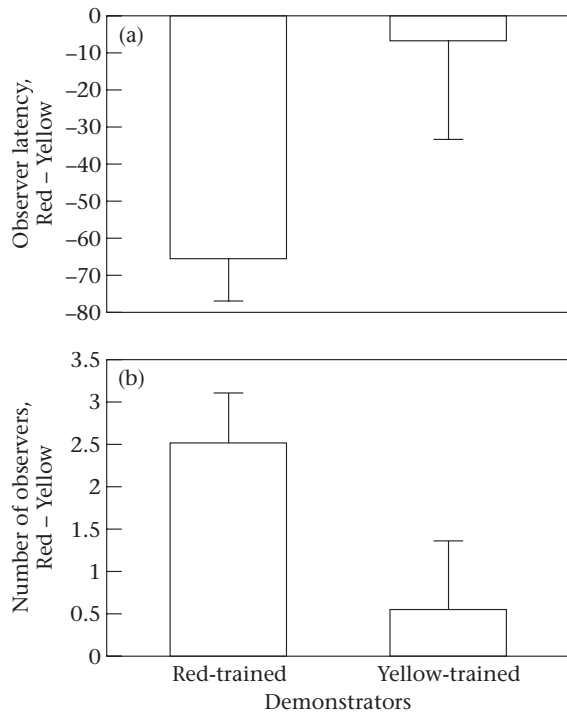
Figure 6. Stage 3 of the trawl-escape experiment, with observers tested after the removal of the demonstrators. Demonstrators had been trained to either the red or yellow escape route. (a) Mean±SE difference between the latencies to enter the red and yellow holes. (b) Mean±SE difference in the number of observers to enter the red and yellow holes.

observers were paired with demonstrators, the training of the demonstrators had a clear effect on the route preferences of the observers. After demonstrators were removed, observers maintained a significant difference in route preference, as measured by the latency to escape. The only plausible explanation for the differences in behaviour between red-demonstrator observers and yellow-demonstrator observers is that the observers had learned a route preference from the demonstrators.

There was no significant difference in the escape times of demonstrators and observers when these individuals were tested together (stage 2), which suggests that the observers followed and accompanied the demonstrators through the escape hole. Laboratory experiments have revealed that naïve observers can learn a foraging or escape route by shoaling with and hence following demonstrators along the route (Laland & Williams 1997; Lachlan et al. 1998; Swaney et al. 2001; Brown & Laland 2002). As a consequence of shoaling with demonstrators that preferentially take one route, observers become more familiar with using this escape hole. Alternatively, or in addition, the demonstrators may draw the observers' attention to one escape route (Swaney et al. 2001). The observers are thus more likely to learn to escape by this route over the alternative route, reflected in the latencies to escape. It is likely that we found a significant difference in latency but not in the number of fish swimming through each hole on stage 3 because individuals were

more hesitant to swim through the hole they had not experienced before, but could discover and swim through this alternative route eventually. Hence the latency measure is a more powerful measure of route preference.

Experiment 2 had a counterbalanced design, so colour preferences cannot be an alternative explanation for our results. The fact that there was a difference in the route preferences of the two groups of observers can be explained only by social learning. However, differential attraction to particular colours could explain why guppies previously paired with red-trained demonstrators demonstrated a stronger preference for the red route than guppies that had been paired with yellow-trained demonstrators did for the yellow route. Rodd et al. (2002), for example, showed that guppies prefer to approach orange and red objects over those of different colours, including yellow.

The current results replicate some of the findings of a similar laboratory trawl experiment using the domestic guppy (Brown & Laland 2002). Brown & Laland found that observers followed pretrained demonstrators through one of two alternative escape routes. Once demonstrators had been removed, the observers no longer conformed to the escape route preference displayed in the presence of demonstrators, although their latency to escape was significantly less than control fish exposed to untrained 'sham' demonstrators. Thus there is evidence for social learning but not for social learning of a particular route. Brown & Laland referred to the loss of the escape route preference in the absence of the demonstrators as 'social release', suggesting that when demonstrators are present, observers are likely to conform to their behaviour (Warburton & Lazarus 1991; Day et al. 2001), but the sudden loss of demonstrator influence causes a collapse in the maintenance of a social tradition. Unlike Brown & Laland (2002), the observers in our study maintained a preference for the demonstrated route after the demonstrators had been removed, escaping through this route more rapidly than the alternative route. However, we did find that the removal of demonstrators weakened the route preference. Wild guppies may be more likely to maintain their preference than the domestic strain because there has been stronger selection to shoal and minimize predation risk. Thus, wild guppies may be more conservative, because it may be costly to try out new, alternative escape responses (see General Discussion).

GENERAL DISCUSSION

We have shown that guppies in the wild can socially learn foraging locations and escape responses by approaching and following conspecifics. These simple social learning processes are likely to be widespread in the wild, because many animals, including invertebrates, fish, birds and mammals, are attracted to conspecifics (Beauchamp et al. 1997). Where alternative routes or patches are easily located, our results suggest that many socially learned behaviour patterns will be rapid and ephemeral, particularly where group composition is unstable and experienced individuals frequently leave the

group. However, where alternatives are difficult or costly to locate, individual preferences learned from others are likely to be maintained for longer.

We could speculate that socially learned foraging patch locations may be more ephemeral than escape routes. When escaping from a predator, the risks of chancing a new, unknown route are likely to be high, compared with making the choice to forage at a new site. If the frequency of individual sampling or exploration is low, the behaviour patterns expressed within a group may be largely determined by the initial choices of a few individuals (Bikhchandani et al. 1998). For example, a group of guppies that happens to be near a rock crevice when a predator approaches may learn this escape route. Other guppies may subsequently learn this escape route from the experienced fish, and subsequently maintain this preference, even though equally adequate escape routes may be available. Such effects have been reported in coral reef fish that use apparently arbitrary traditional mating sites, probably because the costs of detailed individual resource assessment are high compared with the fitness payoff of choosing between the many similar available sites (Warner 1988, 1990).

Even relatively ephemeral learned behaviour patterns may have significant consequences for the behavioural ecology of populations. For instance, local enhancement and social learning are likely to alter the distribution of individuals over resources (Lima & Zollner 1996; Beauchamp et al. 1997). Our results show that the ideal free distribution (IFD) can be disrupted by these processes, at least when resources are new. Discovered food patches are likely to be exploited more rapidly, but the exploitation of initially overlooked patches will be slowed. The ideal free distribution predicts that individuals distribute themselves between patches in proportion to the profitability of the patches (Hart 1993). Male and female guppies foraging in the laboratory conform to the IFD (Abrahams 1989), and Metcalfe & Thomson (1997) noted that animals rapidly distribute themselves between foraging groups according to the predictions of the IFD. These considerations lead to the prediction that similar numbers of fish should be found in each feeder if the test phase continued indefinitely, because the feeders contained similar amounts of food. Hence, there may be a limited window of time in which to observe the effects of local enhancement. An alternative account is that local enhancement, as demonstrated here, may prevent conformity to the IFD. Theoretical models addressing the consequences of local enhancement show that where patches deplete rapidly, foragers do not reach the IFD, and where patches deplete slowly, local enhancement can reduce the fit to the IFD (Beauchamp et al. 1997). Models of habitat choice demonstrate similar effects (Lima & Zollner 1996). Conformity to the ideal free distribution is likely to be slower or more disrupted in high-predation sites than low-predation sites, because discovery of the feeder empty of the artificial shoal may be slowed by a strong tendency to shoal. A stronger effect might therefore be predicted in high-predation sites compared with low-predation sites, a possibility we discuss further below.

Group social dynamics may vary widely between populations of the same species and between species, and are likely to be linked to differences in social learning and social foraging (Cambefort 1981; Box 1984; Coussi-Korbel & Fragaszy 1995; Carlier & Lefebvre 1997). Species or populations that typically dwell in large groups as, for example, an antipredator adaptation may show improved social foraging and escape skills for several reasons. First, individuals may show evolved adaptations to living in large groups, such as paying more attention to the activities of others, because these skills might have greater indirect fitness payoffs when information is readily available from nearby conspecifics (Klopfer 1959; Roper 1986; Lee 1991; Giraldeau et al. 1994; but see Lefebvre et al. 1996; Reader & Lefebvre 2001). Second, development in close proximity to conspecifics may lead individuals to make more use of social information. Third, in species such as guppies that are capable of learning the location of a food patch or escape route through area copying and by following conspecifics (Laland & Williams 1997), processes that enhance group cohesion may also enhance social learning. Evolved adaptations to a high risk of predation, for example, may enhance group cohesion. Thus, several factors may combine to cause between-population differences in social learning propensities.

It is well established that populations of guppies under high risk of predation will shoal more tightly and in larger groups than individuals at low predation risk (see Introduction). Furthermore, laboratory studies have demonstrated that wild adult female guppies from a high-predation site show a greater propensity to follow conspecifics compared with individuals from a low-predation locality (Reader 2000). Both populations preferred to follow a moving artificial shoal through a maze over an identical container empty of conspecifics, but this preference was stronger in individuals from the high-predation site than in individuals from the low-predation site. These findings, combined with the theoretical considerations outlined above, lead us to predict that guppies dwelling in the high-predation sites should show a greater propensity to learn foraging sites and escape routes from conspecifics than fish from the low-predation sites. An interesting extension to our study would be to explicitly address such hypothesized population differences, taking into account other potentially important factors that tend to covary with predation regime, such as population density, food availability or guppy aggressiveness (Magurran & Seghers 1991; Endler 1995).

Our findings reinforce the relevance of laboratory studies (Laland & Williams 1997, 1998; Lachlan et al. 1998; Reader & Laland 2000; Day et al. 2001; Brown & Laland 2002) to the field. Moreover, we show that guppies provide a convenient system for experimental studies of the spread of foraging and predator escape-response information in the wild, an approach that combines the advantages of naturalism with experimental control (Lefebvre & Palameta 1988). The Trinidadian guppy, already a model system for the study of adaptation to local ecological pressures (Endler 1995), may also provide a valuable model for field studies of social learning and simple traditions.

Acknowledgments

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