

Social transmission of maladaptive information in the guppy

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Many animals are capable of learning from others, a process referred to as social learning. There is little doubt that a capacity for social learning is an adaptation and that it typically results in adaptive behavior. What is less clear is whether there are circumstances under which social learning can result in the transmission of outdated, inappropriate, or maladaptive information. Here we report an experimental study that investigated the social learning and transmission of maladaptive foraging information through small social groups of guppies, *Poecilia reticulata*. This experiment used a transmission chain design in which fish in small founder groups were trained to take either an energetically costly circuitous route to a feeder or a less costly short route, with trained founder members gradually replaced by untrained conspecifics. Three days after all the founders had been removed, the behavioral traditions of groups of untrained fish were still strongly influenced by their founder's behavior. Moreover, the rate at which untrained subjects that shoaled with founder conspecifics trained to take the long route learned to take the short route was significantly slower than for fish foraging alone. The results provide unequivocal evidence that maladaptive information can be socially transmitted through animal populations and imply that socially learned information can inhibit learning of the optimal behavior pattern. *Key words*: guppies, information transmission, maladaptation, *Poecilia reticulata*, social learning, tradition. [*Behav Ecol* 9:493–499 (1998)]

It is now well established that social interactions play a major role in the acquisition and development of learned behavior patterns in animals (Galef, 1988; Heyes, 1994; Whiten and Ham, 1992). Field studies have documented the social transmission of novel foraging techniques through natural animal populations (Hinde and Fisher, 1951; Kawai, 1965; Lefebvre and Palameta, 1988). Experimental studies of animal social learning under captive conditions has provided clear demonstrations of social learning in numerous species of animals, as diverse as octopi (Fiorito and Scotto, 1992), chickens (Nicol and Pope, 1994), and chimpanzees (Tomasello, 1996). Such studies have also begun to shed light on the nature of the information transmitted between individuals that guides the learning process (Heyes, 1994; Whiten and Ham, 1992).

There is little doubt that the ability to learn from others is an important adaptation that allows many animals to acquire information concerning foods, predators, and mates at low cost (Bateson, 1988; Giraldeau, 1997; Plotkin, 1988). By learning from others, animals can avoid potentially hazardous learning trials and reduce time spent on exploration (Galef, 1995). There is also little doubt that social learning generates adaptive behavior (Galef, 1995), and much work in the field has been dedicated to understanding the role of social interactions in the development of patterns of behavior that enhance the fitness of free-living animals (Galef, 1996; Giraldeau, 1997). Socially learned behavior patterns may be subjected to fitness trade-offs in exactly the same manner that behavior patterns are acquired through other processes (Stephens and Krebs, 1986), but there is no reason to believe that the behavioral expression of acquired information is less likely

to reflect an adaptive compromise if the information is socially learned.

What is less clear is whether social learning processes in animals can result in the transmission of maladaptive information through a population, that is, information, expressed in behavior, that reduces the fitness of the learner relative to an alternative behavior pattern and that leads to suboptimal behavioral traditions. That social learning processes can result in the transmission of maladaptive information is a conclusion common to several theoretical models that explore the adaptive value of learning from others (Boyd and Richerson, 1985; Feldman et al., 1996; Laland et al., 1996). Such analyses have reached a consensus that social learning is unlikely to be adaptive in temporally or geographically variable environments because the information that is transmitted is likely to be outdated or locally inappropriate. Under such circumstances, reliance on immediate personal experience is a more reliable strategy. The validity of these conclusions, and the assumptions that underlie the models, have been criticized by Galef (1995, 1996), who has suggested that maladaptive information is unlikely to be transmitted or expressed by the learner because both the demonstrator of the behavior pattern and the learner will rapidly adjust their behavior to local conditions.

Although there is considerable evidence that humans can transmit information independent of its fitness consequences (Sahlins, 1976; Montagu, 1980), to date there has been no empirical study investigating whether social learning processes could lead to the transmission of outmoded or inappropriate information through an animal population. Galef has shown that the social learning of dietary preferences in rats that use olfactory cues on the breath of conspecifics was powerful enough to induce rats to consume less palatable and sodium-deficient diets (Galef, 1986). However, Galef's study provides no indication as to whether the suboptimal dietary preference would have been transmitted through a population, as it is well established that a single demonstrator-to-observer social learning episode will not necessarily generate social transmission (Laland and Plotkin, 1990). Tanaka (1995) found that alternative low-efficiency grooming methods were socially

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transmitted down low-ranking matriline of Japanese macaques, but more efficient grooming techniques were found in the high-ranking matriline. However, it is not clear whether there are any fitness costs associated with less efficient grooming in Japanese macaques.

This study is the first attempt to investigate through laboratory experimentation whether maladaptive information can be socially transmitted through animal populations. The approach adopted involves the use of transmission chains, which investigate the passage of information along a chain of individuals. This method was pioneered by Curio in his study of the transmission of mobbing behavior in blackbirds, *Turdus merula* (Curio et al., 1978). Laland and Plotkin (1990, 1992, 1993) have extended the transmission chain approach to the rat, *Rattus norvegicus*, establishing that diet preferences and foraging information can be transmitted along chains of individuals. Galef and co-workers (Galef and Allen, 1995; Galef and Whiskin, 1997) adapted the design to incorporate founder rat populations, which were conditioned to a dietary preference, then gradually replaced by naive conspecifics over a period of time. This has the advantage that the transmission of behavior along a chain can be investigated in a more ecologically valid context (Galef and Allen, 1995).

We have previously established that untrained guppies that swim with trained conspecifics to feed can in the process learn the route to a food source (Laland and Williams, 1997). Fish in small founder groups were trained to take one of two alternate routes of equivalent length to a food source, and then founder members were gradually replaced by untrained conspecifics. Three days after all founder members had been removed, populations of untrained fish still maintained strong preferences for the routes of their founders. This finding suggests that the tendency to shoal may facilitate a simple form of social learning that allows guppies to learn about their local environments. Although there is little doubt that shoaling behavior in the guppy is one component of a coadapted complex of antipredator adaptations (Seghers, 1974), our finding suggests that the transmission of foraging information may be an additional function to shoaling and raises the possibility that social processes that underlie aggregation in other species may also facilitate social learning.

In general, there is a growing body of empirical evidence for social learning in fish. This includes the use of cues from conspecifics to learn to identify predators (Krause, 1993; Magurran and Higham, 1988; Mathis et al., 1995; Suboski et al., 1990), copying of mate choice (Dugatkin and Godin, 1992, 1993), traditionality of mating site preferences, daytime schooling sites, and twilight migration routes (Helfman and Schultz, 1984; Warner, 1988), and the social learning of maze swimming and shuttle-box avoidance tasks (Laland and Williams, 1997; Sugita, 1980; Welty, 1934).

The present study extends our earlier findings to investigate whether maladaptive information can spread through guppy social groups of rapidly changing composition. Founder populations were established, composed of demonstrators trained to take a long or short route to feed, and these fish were gradually replaced by naive fish to investigate whether, and for how long, the route preferences remain. The experiment is an attempt to address two questions: (1) Can maladaptive information be socially transmitted through animal populations? More specifically, the experiment investigates whether socially transmitted information can induce guppies to take a circuitous route to a food site, thereby incurring an energetic cost, when a shorter route is available. (2) Is the rate at which animals learn the optimal behavior pattern in their local environment influenced by social interaction, or is it determined exclusively by patterns of reinforcement in the external environment? In the context of this experiment, we ask whether

fish that swim with conspecifics trained to take the energetically costly route learn to take the optimal route more slowly than fish that swim alone.

METHODS

This experiment replicates our earlier transmission chain study (Laland and Williams, 1997) in which subjects were required to swim, via holes in a dividing partition, from one side of a tank to the other to feed. In contrast to our previous study, however, here the feeder is placed asymmetrically, to generate a long route and a short route, with the long route approximately three times the length of the short route. A pilot experiment (details given below) established that guppies could distinguish between long and short routes and when swimming alone would take the short route significantly more frequently. Founder groups were established with "demonstrator" fish trained to one of two holes in a dividing partition to reach a floating feeder. Gradually the founders were replaced with naive subjects to establish whether the route preferences were maintained. A control group of guppies (the "lone fish") were tested in isolation over 5 days.

Subjects and apparatus

Subjects were 110 adult female guppies, 16 of which were trained demonstrators or founders, 84 subjects in the experimental condition, and 10 subjects in the control condition. Experimental subjects (mean \pm SE = 0.41 ± 0.04 g), control subjects (0.40 ± 0.1 g), and founders (0.38 ± 0.08 g) were of comparable size. An additional 12 subjects took part in the pilot study (size 0.35 ± 0.05 g). All fish were either laboratory reared in the zoology department of Cambridge University or purchased from Neil Hardy Aquatica, London. Female guppies were used because the experimental evidence for social learning is more compelling for this sex (Dugatkin and Godin, 1992, 1993; Laland and Williams, 1997). We used a domesticated strain of guppy because, unlike females from the wild, individual domestic females can be distinguished by their natural color markings. This meant that no artificial marking procedure was required, which is a major advantage, as marking procedures are often extremely stressful and associated with significant levels of mortality.

All fish were housed and tested in glass holding tanks measuring $61 \times 39 \times 30$ cm and maintained at 25°C . During testing, the experimental tank was divided lengthwise by an opaque PVC partition of height 40 cm. Fish were able to swim from one side of the tank to the other via two 8-cm^2 holes in the partition (see Figure 1a). These holes were located 8 cm from the top and 5 cm from each end of the partition. The water level was 31 cm high, 1 cm below the top of the holes. A "trap door" was hinged beside each hole and could be closed by the experimenter by pulling on a string at each end of the tank. The tank was marked to facilitate visual discrimination between the two holes. At one end of the tank, the surrounding to the partition hole was marked with a green, nontoxic, waterproof wax pencil on both sides; at the other end of the tank the hole was marked a contrasting red color.

A second opaque PVC partition, also 40 cm high, was used in the pilot study (Figure 1b). Fish were able to swim from one side of the tank to the other via a single slotlike hole measuring 51×8 cm. This hole was located 8 cm from the top and 5 cm from each end of the partition. Additional pieces of opaque PVC could be attached to the partition centrally to transform the slot into two separate holes of various dimensions (Figure 1b). When the largest additional piece of PVC was in place, the partition had two 8-cm^2 holes in the same positions as the first partition. The surrounding to one of the partition holes was marked with a green, nontoxic, wa-

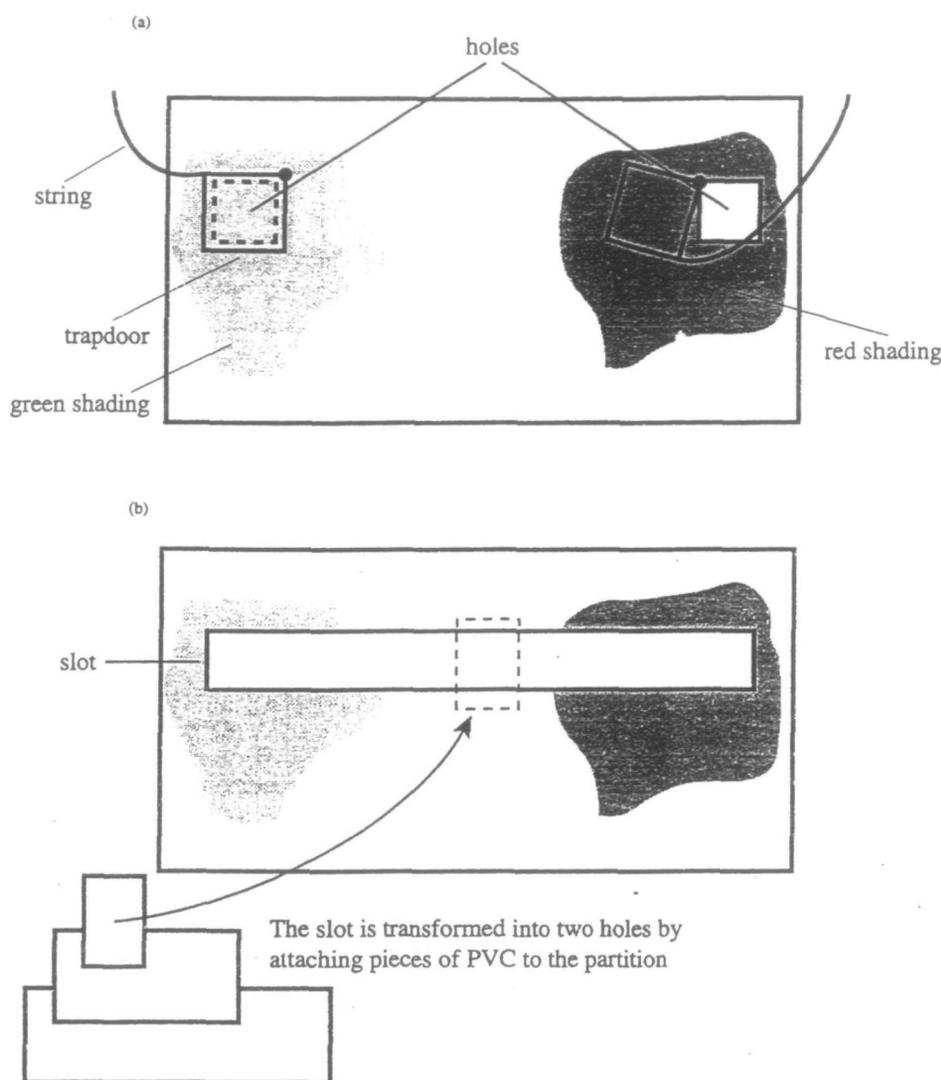


Figure 1

(a) During training and at test, the experimental tank is divided lengthwise by a partition, with two holes through which the fish can swim from one side of the tank to the other. The two holes in the partition are colored red and green to aid visual discrimination. Each hole can be closed with a trap door. (b) A second partition was used during the pilot study. Here fish can swim from one side of the tank to the other through a slot. This slot could be transformed into two holes by attaching an additional piece of PVC centrally. By using attached pieces of increasing size over several days, the partition finally came to resemble that used in the experiment (a).

terproof wax pencil on both sides, while the other was marked red.

Fish were able to feed from floating feeders, which were small, red plastic rings of 3 cm diam and 0.5 cm depth, secured centrally on each of the long sides of the tank. Small quantities of freeze-dried bloodworm (*Chironomus* spp.) could be placed inside the feeders using tweezers, which the fish could access by swimming beneath the ring.

Determining the position of the feeder

Before the experiment was carried out, a pilot study was conducted to determine the most appropriate position for the floating feeder and hence the relative lengths of the long and short routes. Twelve subjects were introduced into the experimental tank, containing no partition, and were fed from a free-floating feeder for 7 days, once-daily. The goal of this procedure was to familiarize the fish with the feeder and to train them to associate the feeder with food. Thereafter, for 10 days, we introduced a partition into the tank for approximately 10 min each time the fish were fed (Figure 1b). For 10 trials each training session, with daily training sessions, the fish were able to swim from one side to the other via the slot in the partition. With each trial the feeder was replaced on the other side of the partition. When the fish were proficient at shuttling from one side of the tank to the other, a small piece of PVC was placed centrally across the slot, transforming

it into two holes (see Figure 1b). Over the next few days, this additional piece of PVC was made increasingly wide, until after 10 days, in its final state the partition had two 8-cm² holes. At this point in the procedure the fish had been trained to shuttle from one side of the tank to the other to feed, via one of the two holes, but had not been specifically trained to favor one hole over the other. Of these 12 fish, we selected the 8 most proficient shuttlers and placed them in a holding tank, while the remaining 4 were removed and took no further part in the experiment.

Each day for the following 6 days the fish were placed singly in the training tank, containing the partition in its final state, and given 10 feeding trials in which they had to swim from one side of the partition to the other via 1 of the 2 holes. On the first day the feeder was centrally located, while each subsequent day the feeder was moved 3 cm toward one or other hole. For four subjects, chosen at random, the feeder was moved toward the red hole, while for the other four the feeder was moved toward the green hole. With each trial, we recorded the hole taken by the fish. The goal of this procedure was to determine the position of the feeder closest to the center where all eight subjects would take the short route significantly more frequently than the long route. For each fish tested over 10 trials, this required them to swim the short route 9 or 10 times (binomial test, $p = .011$)—in other words, to take the short route exclusively or almost exclusively. This

point occurred when the feeder was 15 cm from the central position and just 3 cm from the edge of the short-route hole. Although the feeder was close to the hole, in this position, a subject in the immediate vicinity of the feeder on one side of the partition would not, without moving, be able to see the feeder when it was replaced on the other side of the partition. Moreover, with the long route approximately three times the length of the short route, the pilot study had established that subjects could distinguish between the long and short routes and would take the short route significantly more frequently and almost exclusively.

Experimental procedure

We allocated 84 fish to the experimental condition, 10 to the control condition, and 16 designated founders, at random.

Training of founders. The goal of the pretraining was to train the founders to swim through a hole in the partition (see Figure 1a) to gain access to a feeder on the other side of the tank. We established 12 founder groups of 4 demonstrators. Of these, 8 founder groups were trained to take the long route, with 4 taking the route with the red hole, and 4 the green hole, counterbalanced for position. A further 4 founder groups were established in which fish were trained to take the short route, again counterbalanced for color and position effects. Founders were trained in groups of 4, in their home tanks. Once a day for 7 days founders were allowed to eat from the feeder, floating freely in their home tanks. This exposure was designed to familiarize the founders with eating from the floating feeders. Subsequently, once a day for 21 consecutive days the founders were trained to swim through their target hole to the feeder, where they were allowed to eat a small amount of freeze-dried bloodworms, equivalent to two or three food items each. Founders trained to take the red hole were allowed to swim through this hole, but not the green hole, the trap door being closed by the experimenter if the fish approached the hole (see Figure 1a). Similarly, the fish trained to take the red hole were allowed to swim through the red, but not the green, hole. The fish responded to the closing of the trap door as they would to a mild aversive stimulus, rapidly swimming away from it. We then transferred the feeder to the other side of the partition, and the fish were required to swim back through the same hole to feed again. Each day's training was completed when the fish had shuttled from one side to the other 10 times. In the early stages of training the floating feeder was placed close to the target hole, but as founders became more familiar with the task, the feeder was moved progressively toward the asymmetrical experimental position. By the end of the training period, founders swam rapidly from one side of the tank to the other via the target hole and fed at the feeder. The partition was removed when the daily training of 10 trials was completed and reintroduced when training started the following day. Because all the founder groups were not established simultaneously, founders were reused in the experiment. After being used as founders, these fish received further training until their shuttling from one side of the tank to the other was equivalent to what it had been before their use.

Pretraining of subjects. Before testing, subjects in the experimental and control conditions were fed in their home tanks from a free-floating feeder for 7 days, once-daily. This was designed to familiarize them with the feeder.

Testing. Subjects were assigned to four experimental conditions, which had founders trained to take the short or long routes, and where each could be fed via the red or green hole. We placed a single observer fish in each tank 24 h before the start of the experiment with a group of four founders. We started the experiment by introducing the partition into the experimental tank. All fish were allowed to swim freely

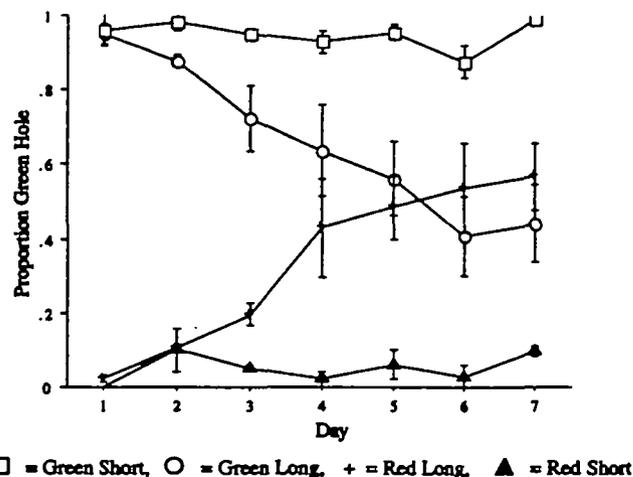


Figure 2

Proportion (mean \pm SE) of times that experimental subjects take the green hole to feed for fish with founders trained to take green or red routes, and where the trained route could be long ($n = 4$) or short ($n = 2$).

throughout the tank and were given uninhibited access to both holes. Fish were free to feed at the floating feeder, on the opposite side of the partition. For each of 10 trials, the experimenter recorded which (if any) hole each fish swam through, whether it fed at the feeder, and at what time it fed. After each trial, the feeder was placed on the opposite side of the partition, and a new trial began. When the trials were completed the partition was removed. A single founder was taken out of the tank and replaced by a second naive subject. The following day and for 7 days in total, the trials were repeated. Each day, after 10 trials a fish was removed from the tank and replaced with a naive fish. For the first 4 days one of the founders was removed, so that on day 5 of the experiment none of the fish in the tank had received any training from the experimenter. From days 5 to 7, the subject that had been in the tank the longest was removed and replaced with another naive fish. The testing procedure for subjects in the control condition was identical, but we housed and tested these subjects in isolation.

RESULTS AND DISCUSSION

To avoid problems associated with the non-independence of subjects in shoals and of shoals from one day to the next, we analyzed only the data from the newest fish placed in each enclosure each test trial. An ANOVA was carried out with three independent variables, route length (long or short), route color (green or red), and day of testing (1–7). The results are presented in Figures 2–4.

The key finding is that on day 7 there were significant differences between subjects in the green short and red long conditions, despite being exposed to an identical apparatus and procedure ($t = 3.01$, $df = 4$, $p < .05$). There are comparable differences between subjects in the green long and red short conditions ($t = 3.44$, $df = 4$, $p < .05$). This indicates that subjects with founders trained to take the long routes do acquire a tendency to take a circuitous route from their founders.

Fish with founders trained to take the green route took the green route significantly more frequently than fish with founders trained to take the red route ($F_{1,36} = 177.8$, $p < .001$) (see Figure 2). Fish with founders trained to take a short route acquired a preference for this route and maintained this pref-

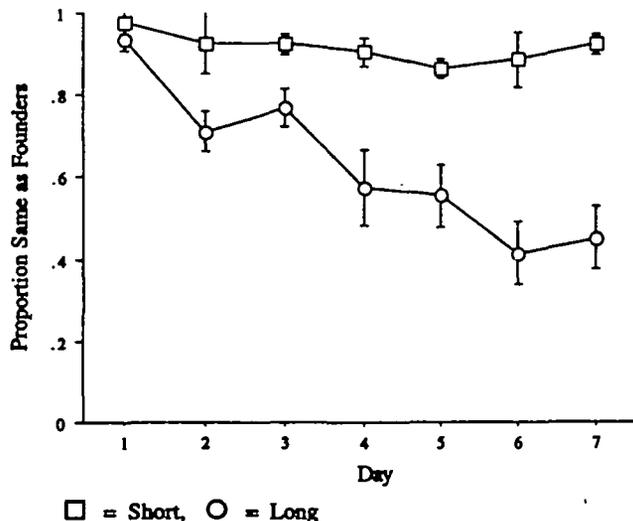


Figure 3
Proportion (mean \pm SE) of times that experimental subjects took the same hole as their founders over 7 days. The route preference traditions are much more stable for populations with founders trained to take the short route ($n = 4$) than for populations with founders trained to take the long route ($n = 8$).

erence even when all of the trained fish had been removed. Fish with founders trained to take a long route exhibited a decline in their preference for this route, and by day 7 were using both routes equally. These findings are reflected in a significant route color-by-route length interaction ($F_{1,56} = 51.7$, $p < .001$), with the route color effect stronger in subjects with founders trained to take the short route ($F_{1,56} = 155.9$, $p < .001$) than in subjects with founders trained to take the long route ($F_{1,56} = 27.9$, $p < .01$). On day 7, there was a significant difference in the proportion of times that subjects in the green short and red short conditions took the green route ($t = 16.93$, $df = 1$, $p < .05$), but no significant difference among subjects in the green long and red long conditions ($t = 0.62$, $df = 6$, $p > .1$).

Fish with founders trained to take the short route took the short route more frequently than fish with founders trained to take the long route ($F_{1,56} = 50.5$, $p < .001$). This effect was still significant on day 7 ($t = 4.29$, $df = 10$, $p < .01$).

The stability of the traditions for taking one or the other route is illustrated in Figure 3, which presents the proportion of times that experimental subjects took the same hole as their founders over 7 days. The route preference traditions are much more stable for groups with founders trained to take the short route, which show no decreasing trend in performance ($F_{1,70} = 1.507$, ns), than for groups with founders trained to take the long route, which exhibit a significant decay ($F_{1,70} = 53.95$, $p < .001$).

We examined the longevity of the route preferences within individuals by taking the data from those fish that had spent 5 days in the tanks, excluding founders, and investigating how their route preferences changed over time. The longevity of route preferences among individuals trained to take the long route was compared with the performance of the "lone" fish in the control condition (Figure 4). Shoaling fish with founders trained to take the long route acquire a short route preference considerably slower than lone fish (repeated-measures ANOVA, $F_{1,52} = 30.36$, $p < .001$). Even after 5 days in the tank, fish with founders trained to take the long route take the short route less frequently than lone fish on their first day. Thus shoaling appears to have inhibited learning of the optimal route to feed.

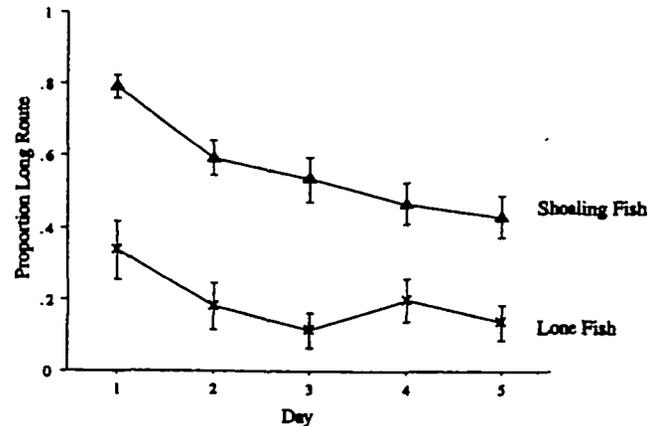


Figure 4
The longevity of route preferences within a subject, scored as the proportion (mean \pm SE) of occasions that subjects took the long route. Shoaling fish in the experimental condition ($n = 24$), with founders trained to take the long route, acquire a short route preference slower than lone fish ($n = 10$) in the control condition.

Whether or not it is appropriate to describe as maladaptive the traditions and socially transmitted information of groups with founders trained to take the long route depends critically on the assumption that there is a cost associated with taking this route. There are three reasons we believe the long route is associated with a significant energetic cost relative to the short route. First, fish in the pilot study expressed a marked preference for the short route. The behavior of these pilot study fish cannot be explained in terms of route location or color preferences (because these variables were counterbalanced), nor in terms of patterns of shoaling or the presence of conspecifics (because these fish were tested in isolation). Subjects in the pilot study, if positioned in the immediate vicinity of the feeder on one side of the partition, would not, without moving, be able to see the feeder when it was replaced on the other side of the partition. On the final days of the pilot study, these fish swam directly and rapidly toward the target hole on each trial. Hence, the preference for the short route exhibited by these fish cannot be explained as simply reflecting the fact that the fish could see the feeder and swam toward it. The fish in the pilot study were required to learn to swim toward a particular hole at a particular location in the tank. If taking long and short routes involved expending equivalent amounts of energy, we would not expect to see the fish in the pilot study consistently preferring the short route. Second, by similar logic, if taking long and short routes involved expending equivalent amounts of energy, we would expect populations with founders trained to take the short route to have exhibited a decline in their preference for the short route, but they did not. Third, taking the short route when the rest of the population took the long route would give an individual unimpeded access to the food in the feeder during the extra time it took the others to reach the feeder. Thus, for populations in which some fish took the long and some the short route, fish swimming the short route were likely to consume more food in total than fish swimming the long route. On a substantial number of trials (49 out of 840, or 6%), an individual fish did take the short route alone, and in virtually all such instances it began feeding several seconds earlier and almost certainly consumed more food items than its shoal members as a consequence (although the number of food items consumed by each subject was not recorded). Indeed, the short route was so short that, were subjects in the vicinity of the feeder to swim a short distance toward the end

of the tank and orient themselves toward the hole, they would frequently be able to see the feeder through the hole when it was replaced on the other side of the partition. On a surprisingly high number of occasions, even experimental subjects with no prior conditioning oriented themselves toward the hole where it would appear they could see the feeder, and yet still swam the long route, through the alternative hole, with the rest of the group. Unlike a social forager faced with the decision of whether to switch patch, as the floating feeders always contained approximately the same amount of food, here switching to the short route is unlikely to be associated with uncertainty about rates of reward. For these reasons we believe there is a significant energetic cost associated with taking the long route to feed.

The theoretical analyses mentioned in the introduction reached the conclusion that social learning is unlikely to be adaptive in rapidly changing environments because the information transmitted may be outdated, a conclusion that has incited some controversy (Feldman et al., 1996; Galef, 1995, 1996; Laland, 1996). This experiment was designed to test this theoretical finding. Here the long-route conditions represent an environment in which the optimal route to feed has suddenly changed. Traditions for taking a particular color route will thus have to adjust and track this change by switching route preference. The experiment investigates whether swimming with other fish that had a prior preference for one route (the founders) slows down the rate at which subjects adjust to the new patterns of reinforcement in their environment relative to fish that swim alone. Consistent with the theoretical predictions, shoaling fish adjusted more slowly than lone fish.

The findings of this experiment should be interpreted with some caution. While the experiment can legitimately be described as providing evidence for the social transmission of maladaptive information, neither the behavior of the fish nor the general capacity for social learning should be described as maladaptive. Taking an energetically costly route may well be an adaptive strategy to animals that gain protection through aggregation, provided that conspecifics are taking the circuitous route. For shoaling fish, swimming alone can be associated with a significant increase in the risk of predation (Pitcher and Parrish, 1993). It may well be adaptive for individual guppies to swim the long route with conspecifics than to risk the short route alone. Such fish are effectively required to size up the relative fitness gains associated with shoaling versus the alternative gains of unimpeded access to a food site, and this balance will vary from one individual to the next. Furthermore, although in this instance the information transmitted between fish in the long-route conditions was suboptimal, in general there is no doubt that animal social learning is typically adaptive and results in the transmission of good information (Galef, 1995). This is because the germane features of the environment are frequently sufficiently stable to afford equivalent levels of reinforcement to the transmitter and receiver of information. However, the behavioral tradition for taking the long route could be described as maladaptive because if all of the members of the population were to switch to the short route, they would all have to expend less energy in locating food, and their search time would be reduced. Thus the behavioral tradition favoring the long route is associated with a potential reduction in the long-term rate of net energy gain relative to a tradition favoring the short route.

Although the experiment lasted only 7 days, there is little reason to doubt that, if it continued, the performance of fish in the green short and red long conditions would have converged, with all fish eventually taking the shorter green route. Similarly, we would anticipate that the red short and green long conditions would also have converged, with all fish even-

tually taking the shorter red route. The greater decay of traditions for the longer route illustrated in Figure 3 indicates how, in a relatively constant environment, social learning will typically generate adaptive behavior. Eventually the traditions will converge on the optimal foraging behavior, and such traditions will remain stable in the face of consistent positive reinforcement favoring the optimal solution. Thus in a constant, or slowly changing, environment, it is unlikely that maladaptive patterns will persist, and it is consequently unlikely that social learning will produce populations that differ in behavior with one behaving less adaptively than another. This reasoning is consistent with the findings of several studies of fish populations that the presence of conspecifics accelerates the learning of novel tasks or the efficiency of foraging (Pitcher et al., 1982; Pitcher and House, 1987; Sugita, 1980; Welty, 1934). However, in a changing environment, socially transmitted traditions may constantly trail behind the environmental state because there may not be enough time to adjust to the optimal before a new behavior pattern becomes best. As Figures 2 and 4 illustrate, if the environment were to change rapidly, the behavioral traditions would lag behind the environmental state, with the lag greater for animals that aggregate and rely on social information than it would be for isolated animals relying exclusively on their own experience. If this is the case, suboptimal traditions may be fairly common in animal populations.

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