The effects of group size, rate of turnover and disruption to demonstration on the stability of foraging traditions in fish

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There is considerable laboratory-based evidence that social learning plays a role in the behaviour of many animals, including fish. However, a weakness of such studies in fish, is that in virtually all to date, the behaviour showed could be learned asocially, with the social influence merely accelerating the rate of learning. Lefebvre & Palameta (1988. *Social Learning: Psychological and Biological Perspectives*. pp. 141–164) argued that the most compelling evidence for social learning comes from studies where inexperienced animals are unlikely to learn the target behaviour by themselves. The present study is designed to address this concern, by employing a feeding tube task in which fish gain access to food by swimming in a manner that they would not normally show. Employing a transmission chain design, we show foraging traditions in guppies, *Poecilia reticulata*, and southern platyfish, *Xiphophorus maculatus*, in which shoal members continue to exploit the food available in the feeding tube, in spite of changes in the composition of the shoal due to the gradual removal of demonstrators. Two experiments provide strong evidence for social learning underlying traditional behaviour, such as migratory routes, in fish, and reveal how the stability of such traditions (duration within a population) is affected by group size (2, 4 or 6 fish) and rate of turnover (16.5%, 25% or 50% per day). While larger shoals of fish showed more stable traditions than smaller shoals, this was found to be related to their slower rate of turnover rather than a direct effect of group size.

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In making decisions, such as how to find food and mates, or avoid predators, many animals use information that is produced by others. The term 'social learning' refers to any such incidence in which individuals acquire new behaviour or information about their environment via observation of, or interaction with, other animals, or their products. Over the last 20 years, the study of social learning has expanded greatly and is now a major topic of research in ethology, behavioural ecology and comparative psychology (Galef & Giraldeau 2001; Shettleworth 2001). Research over the last 50 years has showed that social learning is common amongst fish, birds and mammals, and should now be regarded as a regular feature of vertebrate life (Lefebvre & Palameta 1988; Heyes & Galef 1996).

Small laboratory fish are particularly amenable to social learning experimentation, being cheap and easy to house in aquaria, allowing the multiple replicate populations necessary for good statistical power in the analysis of socially transmitted behaviour. Documented cases of social learning in fish are now commonplace (Brown & Laland 2003, 2006), and there is strong laboratory- and field-based evidence that social learning plays a role in the antipredator behaviour, migration and orientation, foraging and mate choice of fish (Helfman & Schultz 1984; Pitcher & House 1987; Magurran & Higham 1988; Suboski & Templeton 1989; Ryer & Olla 1991; Dugatkin 1992; Laland & Williams 1997, 1998; Reebs 2000; Brown & Laland 2001; Day et al. 2001; Witte & Ryan 2002).

Many fish appear to show traditional use of feeding, resting, schooling or mating sites, where knowledge concerning the use of particular locations for specific functions, or of migration routes to and from such locations, is socially transmitted between individuals (Helfman & Schultz 1984; Warner 1990; Brown & Laland 2003). The

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mechanisms underlying these traditions have been investigated in the laboratory using transmission chain studies (Laland & Williams 1997, 1998). Such studies simulate natural traditions by training a population of founders to perform a task, and gradually replacing these experienced individuals with naïve animals, testing whether the original behaviour remains in the population in spite of this change in personnel. Transmission chain studies have been employed successfully to investigate traditional aspects of bird mobbing behaviour, rat foraging and chimpanzee tool use (Curio 1988; Laland & Plotkin 1990, 1992, 1993; Galef & Allen 1995; Whiten et al. 2005). For instance, Curio (1988) describes how blackbirds can be conditioned to mob an arbitrary stimulus, and how this mobbing behaviour can be socially transmitted along a chain of birds. Similarly, Whiten et al. (2005) show that alternative tool-using behaviour can be socially transmitted through captive chimpanzee groups.

One potential criticism of many laboratory experimental studies of social learning in fish, including the aforementioned transmission chain studies, is that the behaviour showed could easily be learned asocially. This concern is particularly relevant to fish maze-learning studies (Reader & Laland 2000; Swaney et al. 2001), where individual fish might be expected eventually to learn to swim a maze to locate food, and social interaction may merely enhance the rate of their learning. Moreover, given that to solve the maze, an individual fish is not required to show any novel motor pattern, there is no behavioural cue that is indicative of social learning. Lefebvre & Palameta (1988) argued that the most compelling evidence for social learning comes from studies in which inexperienced animals are unlikely to learn the target behaviour by themselves. Indeed, the field of social learning shows a long tradition of emphasis on the importance of behavioural novelty for demonstrations of specific forms of social learning, particularly imitation (Thorndike 1911). We know of no published studies, however, of social learning in a fish species where a task that is difficult to learn asocially has been employed.

The present study is designed to address this concern, by employing a feeding tube task in which fish gain access to food by swimming directly up a vertical tube with a diameter only marginally greater that their body circumference. Pilot studies established that: (1) inexperienced fish virtually never solved this task without observation of an experienced conspecific; (2) the solution to the task required the fish to swim in a manner that they would not naturally show, and which could be regarded as an indicator of a social influence on learning. The observation of foraging traditions in which individuals continue to exploit the food available in the feeding tube, in spite of changes in the composition of the population, would provide strong evidence for social learning underlying traditional behaviour in these fish.

In addition to the objective of investigating whether such traditional behaviour can be established, we also set out to shed light on the factors that affect the stability of traditional behaviour in animals. Several factors have been identified that affect the duration and transmission fidelity of transmitted information. Laland & Plotkin (1992) found that the social transmission of information concerning buried food in Norway rats, *Rattus norvegicus*, was enhanced by opportunities for practice, while the transmission of dietary preferences was reinforced by a predisposition for the transmitted diet and undermined by a predisposition for an alternative diet (Laland & Plotkin 1991, 1993). Galef & Whiskin (1997) found that the stability of an experimentally induced food avoidance tradition decreased in fidelity with increased group size.

Here, we focus on three potential factors affecting transmission stability, namely, disruption in demonstration, group size and rate of turnover. If short-term fluctuations in the availability of resources, the temporary presence of predators, or adverse conditions interrupt the performance of traditional behaviour, the fidelity of information flow could be impaired. Such instability might suggest that natural animal traditions are highly vulnerable to perturbation and likely to show regular change. Conversely, if the fidelity of information transmission is unaffected by such interruptions, animal traditions might be expected to be relatively stable. To explore this possibility, experiment 1 introduces a hiatus in demonstration and explores its impact on information transmission. Group size is another factor mooted to affect the stability of animal traditions (Galef & Whiskin 1997), but the generality of Galef & Whiskin's (1997) finding of a negative relationship between group size and stability has yet to be established. Experiment 2 compares the fidelity of information transmission in shoals of 2, 4 or 6 fish. However, if, in the transmission chain, demonstrators are replaced at a constant rate, group size becomes confounded with rate of turnover, since replacing a single demonstrator in groups of sizes 2, 4 and 6 constitutes a turnover of 50%, 25% and 16.5%, respectively. Accordingly, in experiment 2 we introduce a fourth experimental condition, of group size four and with two individuals replaced (50% turnover), which, in comparison with the other conditions allows us to disassociate these two variables, and explore their significance independently.

EXPERIMENT 1: SOCIAL TRANSMISSION OF A NOVEL FORAGING BEHAVIOUR IN A POPULATION OF GUPPIES OF CHANGING COMPOSITION

Here we used a transmission chain design to investigate whether a novel foraging behaviour could be retained in small populations of guppies, *Poecilia reticulata*, in spite of gradual changes in the populations' composition. Founder populations of fish were established composed of individuals that had been trained to swim up a vertical tube to receive a food reward. Over the course of the experiment, these founders were periodically replaced with individuals that had no experience of the tube feeding behaviour, and when all the founders were removed, we systematically replaced the individuals with the most experience of the task. We investigated whether, and how, the latency to feed, and percentage of individuals that successfully show the feeding behaviour, changed in the face of these manipulations of population structure. In addition, we set out to explore the robustness of these traditions in the

face of perturbations, such as a temporary disruption in the opportunity to carry out the task, by introducing experimental conditions with and without a short break in demonstration.

Methods

Subjects and apparatus

In total, 182 adult male guppies were used in this experiment, of which 130 were bred from mixed wild Trinidadian stock in aquaria at the University of St Andrews, and a further 52 were purchased from Neil Hardy Aquatica, London. The domestic guppies were used due to a temporary unavailability of wild-type fish. The experiment was carried out in two separate batches, with fish of each strain (wild type/domestic) distributed across conditions where possible although the domestic strain was absent from the hiatus condition. Each population was composed of a single fish strain. Below we describe the statistical analyses investigating the effects of strain (see below). Adult male guppies were used, as their diverse coloration allows for the precise identification of individuals without the use of stressful marking procedures. In total, 36 fish were used as trained founders, in nine groups of four individuals, and a further 20 as untrained founders, in five groups of four. The remaining fish acted as observers during the experiment, and were experimentally naïve.

Prior to the training period, all the fish were housed together in a glass holding tank (91 × 29 cm and 39 cm high) with a water depth of 25 cm, maintained at 25°C. Throughout the experiment the fish were kept on a 12:12 h light:dark cycle, with lights on at 0700 hours. Every evening (at ca. 1730 hours), all fish were fed with standard aquarium tropical fish flaked food. Experimental populations of four fish were housed in six smaller tanks (61 × 39 cm and 30 cm high), three with trained and three with untrained founders. Each tank contained a combination charcoal filter/aerator or an electrical filter with a separate aerator. Opaque screens were placed between the tanks to prevent visual interaction between populations.

The feeding tube consisted of a 100 mm long opaque PVC cylinder (internal diameter 32 mm), closed at one end and open at the other (see Fig. 1). The tube contained a transparent viewing window (26 × 15 mm) at the closed end, positioned adjacent to the side of the tank, to allow confirmation by the experimenter that the fish were feeding. The window was situated so that fish could not see the food from outside the feeding tube, and was covered with transparent plastic and tightly sealed so that no possible odour cues would attract fish to the window rather than the bottom of the tube. A wire hook allowed the feeding tube to be attached to the edge of the tank. Blocks (5 mm³) of freeze-dried *tubifex* were used as food. When inserted into the vertical tube, these blocks would float against the top lid and did not sink or disintegrate during the experiment. When oriented in a vertical position, fish could only enter the feeding tube via the bottom aperture and were required to swim vertically the length of the tube to access the food (Fig. 1a).
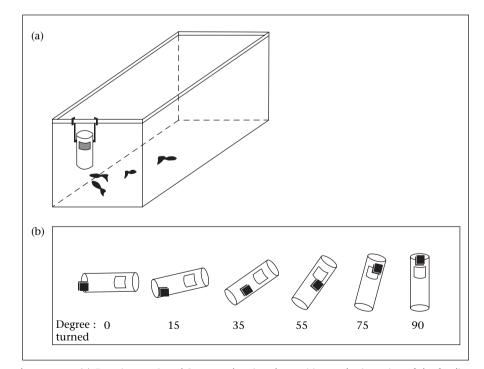

Figure 1. Experimental apparatus. (a) Experiments 1 and 2 set-up showing the position and orientation of the feeding tube. Entrance to the tube was at the base and fish were required to swim up and be observed to feed from the viewing window to class as feeding successfully. (b) Procedure for training of demonstrator founders. Over several trials, the feeding tube was rotated, and the food inserted into the tube, in a step-by-step fashion, gradually shaping the fish to feed by swimming vertically up the tube.

Procedure

Trained demonstrator founders were shaped to feed from the feeding tube over the course of several training trials. Initially, the feeding tube was affixed to the side of the tank and oriented horizontally, four inches below and parallel with the surface, with a *tubifex* block placed in the mouth of the tube. When the fish had become proficient at feeding from the apparatus, in the next training trial the tube was rotated slightly towards the vertical and the food placed slightly further up its length. When the fish become proficient at feeding from this new orientation, the tube was rotated further. This process was repeated until the demonstrators were swimming up and feeding from the vertically positioned tube (Fig. 1b). The entire training took 11 days to complete, with two training trials a day, at approximately 0900 and 1600 hours.

Untrained founders in the control condition experienced the same procedure but with an absence of *tubifex* cubes. This ensured that both demonstrator and control founder populations were equally accustomed to the presence of the tube and the disturbance involved during the placement and removal of the tube during trials, but that founders in the experimental condition alone were experienced at feeding from the tube.

Once trained, the populations were then subjected to two feeding trials per day over a 10-day period. The trials took place between 0900–1100 hours and 1530–1730 hours. The order that the tanks were tested in was rotated each day. Each trial lasted 10 min and was started by attaching the vertical feeding tube to the side of the tank and adding the *tubifex* cube. At the end of the trial, the feeding tube and food were promptly removed. The identity of, and time taken by, any fish that completed the task during the trial was recorded. Fish were only considered to have completed the trial successfully if they swam right up to the top of the tube and fed.

Each day, after the second trial of the day, all fish were fed a small amount of standard flake food, and one fish was removed from each tank, and replaced with a naïve subject from the holding tank. The four founder fish were removed and replaced first, chosen at random, and when all of them were removed, we replaced the fish that had been in the tank the longest. In batch 1, a 2-day hiatus in this experimental procedure was introduced after 5 days of testing, during which period the fish received no training and no flake food. Batch 2 of the experiment was conducted using the methods described above, but without the 2-day break in the transmission chain.

Statistical procedures

We calculated the within-tank median latency to complete the task (or mean number of task completions) per trial and then derived the mean of the median latencies (or number of task completions) across the relevant number of trials (see Results and Discussion) for each tank. We used ANOVAs (analysis of variance) on these mean values, unless parametric assumptions were violated. Transformations are stated if used and all relevant tests were two tailed. Fish that failed to complete the task were assigned a ceiling value of 600 s. The effect of the hiatus was tested using data from trials after the break (i.e. trials 11−20). Post hoc tests used Tukey HSD and all statistics were generated using R (version 2.4.0).

Results and Discussion

We found a significantly lower latency to complete the task in populations that were seeded with trained demonstrators than control populations (Wilcoxon: $W = 0, N = 14$, $P = 0.003$; Fig. 2). There was no effect of either guppy strain (Wilcoxon: $W = 23.5, N = 14, P = 0.671$) or hiatus within test condition (ANOVA: $F_{1,7} = 0.770, P = 0.409$) on the latency. We tested further the effect of the hiatus by investigating, in 12 guppies that had previously completed experiment 1 (in batch 2), the latency to complete the task before and after an additional 48-h 'hiatus', but found no significant difference (Wilcoxon paired comparison: $V = 20, N = 12$,
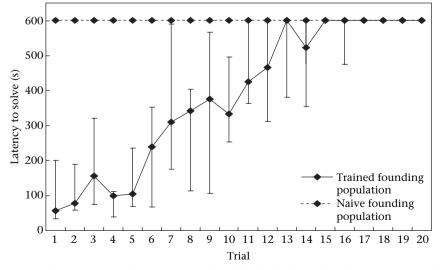

Figure 2. The median ± IQ range latency to solve the task across tanks (for both batches), plotted against trial, in the test condition (trained founders: $N = 9$) and control condition (naïve founders: $N = 5$).

$P = 0.8336$). These fish were tested independently and in visual contact of three naïve conspecifics (behind a transparent screen) to minimize stress.

Similar results were obtained using the average latency, calculated over the median latency per tank, across trials 9–20, after the founding population had been replaced (trained versus naïve founding population: $W = 7$, $N = 14$, $P = 0.044$; guppy strain: $W = 32$, $N = 14$, $P = 0.102$; hiatus: $W = 23$, $N = 14$, $P = 0.898$). Hence, the latency effect resulted from social learning.

The results provide evidence that information that is difficult for individual fish to learn asocially can readily be learned socially and can be transmitted along chains of individuals in a population of changing composition. This retention of information along the chain requires that naïve individuals learn from demonstrators that themselves acquired the information using social learning. The absence of any disruptive effect of the hiatus suggests that such traditions could be relatively stable in more naturalistic circumstances. Further investigation, involving hiatus of increasing duration, would however be an interesting avenue for future research.

EXPERIMENT 2: THE EFFECT OF POPULATION SIZE AND TURNOVER ON THE STABILITY OF A NOVEL FORAGING TRADITION

Here we set out to explore how the stability of the feeding tube foraging tradition is affected by group size, repeating the experimental procedure in populations of fish of different sizes (2, 4 and 6 fish). However, if founders are replaced one at a time, large groups will take longer than small groups to experience a complete replacement of trained founders, creating a confound to group size in the form of turnover rate. We addressed this problem by investigating the stability of transmission in groups of size 2, 4 and 6, with daily replacements of a single fish, but introducing a fourth condition, in which groups of size four experience double the rate of replacement (i.e. two fish replaced each day). This allows us to disassociate the effects of population size and turnover rate on transmission stability.

Methods

Subjects and apparatus

The experiment was conducted on 304 adult southern platyfish, *Xiphophorus maculatus*, obtained from Ultimate Aquatics, Cupar, U.K. Fish were kept in two holding tanks (91 × 29 cm and 39 cm). Following pilot studies, which revealed within-strain assortment in shoaling, salt and pepper and calico morphs were chosen for the experiment. Both of these strains' coloration was uniform enough to facilitate significant within-strain social interaction while also displaying sufficient variation to allow easy identification of individuals. Each population was composed of a single strain, with strain balanced across conditions as far as possible. However, the calico morph was disproportionately represented in the size = 2 condition. Prior to experimentation, the coloration and markings of each fish were recorded. We used single-sex populations to remove

the disrupting effects of sexual activity on the foraging behaviour. Forty-eight demonstrator founders were trained to show the feeding behaviour using the method described in experiment 1, forming four sets of founder populations of sizes 2, 4, and 6 individuals. These conditions will be referred to as size = 2, 4 and 6, respectively. Furthermore, 48 untrained demonstrators received experiences as described for the control condition in experiment 1. In these conditions, the experimental procedure was the same as experiment 1 (replacing one individual after every two trials, at the end of each day), except that the experiment lasted 7, instead of 10, days and there was no 48-h hiatus. The experiment was carried out in three batches.

Four more populations, each consisting of four platys, were allocated to a fourth condition, which we refer to as the 'double replacement' condition. Here, two individuals were replaced after every two trials, so as to afford the same replacement rate, and same amount of observation time, as the populations containing two fish.

Results and Discussion

We found a significant difference between the four conditions in the median latency to complete the task ($F_{3,12} = 23.076$, $P < 0.001$). The latency was significantly longer in the size = 2 condition than either the size = 4 or size = 6 conditions (size = 4: $P = 0.001$, size = 6: $P < 0.001$), while there was no significant difference in latency between the size = 4 and size = 6 conditions ($P = 0.690$; Fig. 3a). We found similar results when comparing the mean latency across trials after the founding population had been removed ($F_{3,12} = 32.401$, $P = 0.004$; size = 2 versus size = 4: $P = 0.042$; size = 2 versus size = 6: $P = 0.014$; size = 4 versus size = 6: $P = 0.923$).

Similarly, we found a significant difference between the four conditions in the mean number of task completions per fish ($F_{3,12} = 50.021$, $P < 0.001$). There were significantly fewer task completions in the size = 2 condition than either the size = 4 or size = 6 conditions (size = 4: $P < 0.001$, size = 6: $P < 0.001$), while the difference in number of times the task was completed between the size = 4 and size = 6 conditions only approached significance ($P = 0.08$; Fig. 3b). We found similar results when comparing mean number of task completions across trials after the founding population had been removed, although here, the group size effect was also significant between conditions size = 4 and size = 6 ($F_{3,12} = 32.401$, $P < 0.001$; size = 2 versus size = 4: $P < 0.001$; size = 4 versus size = 6: $P < 0.001$).

In contrast, post hoc analysis (Tukey HSD) revealed that there was no significant difference in the latency or number of task completions between the size = 2 condition and the 'double replacement' condition (latency: $P = 0.998$; feeds: $P = 0.825$; Fig. 3). Similar to the size = 2 condition, the latency of the 'double replacement' condition was significantly longer, and showed significantly fewer task completions, than either the size = 4 or size = 6 conditions (latency: size = 4: $P < 0.001$, size = 6: $P < 0.001$; feeds: size = 4: $P < 0.001$, size = 6: $P < 0.001$).
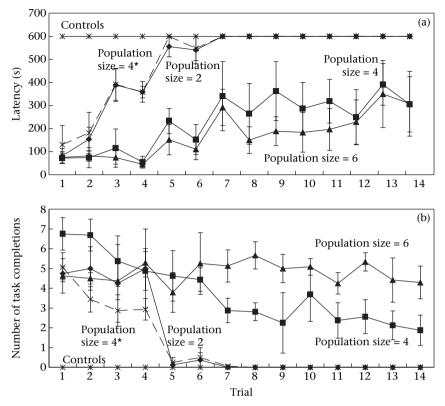
Figure 3. The mean ± SE of (a) the latency to solve the task (s), and (b) the number of task completions per fish, across tanks, for each of the group size conditions. 4* Denotes the double replacement condition.

Similar results were obtained when comparing mean values across trials, calculated across the median latencies per tank, for which the founding population were absent (latency: size = 2 versus 'double replacement': $P = 1.000$; 'double replacement' versus size = 4: $P = 0.038$; 'double replacement' versus size = 6: $P = 0.013$; feeds: size = 2 versus 'double replacement': $P = 0.954$; 'double replacement' versus size = 4: $P = 0.002$; 'double replacement' versus size = 6: $P < 0.001$). The task was not solved in any of the three control conditions. The failure of any fish in the control conditions to solve the task clearly shows that the transmission of the feeding behaviour across trials in the experimental conditions is indicative of social learning.

The findings shed light on the role of two factors that may affect the stability of socially transmitted information. First, the fidelity of information transmission appears to increase with increasing group size. In the largest groups (size = 6), the number of task completions remained constant across trials, and the latency to complete the task only increased slightly, indicative of relatively stable transmission. Conversely, in the smallest groups (size = 2), the number of task completions diminished, and latency to complete the task increased, rapidly with increasing trials. If the number (rather than the proportion) of individuals replaced per trial is constant across different group sizes, the rate of loss of information is negatively related to group size. In larger compared to smaller groups, initially there are more trained individuals and their frequency diminishes at a slower rate (i.e. over

more trials), resulting in a greater opportunity for naïve individuals to learn. Furthermore, for a naïve individual to learn the task socially once the founding population has been replaced, on average the information will have to be transmitted, from the ancestral trained founding population, along a chain of fewer individuals in a large group than in a small group. In other words, in any trial after the removal of the founding population, there is a higher 'cultural relatedness' between an individual that socially learns the task and its trained cultural ancestor in a large group than in small group. If there is imperfect fidelity of transmission between each link in the transmission chain (i.e. between cultural parents and offspring), there will be a slower rate of extinction of the information in large groups than in a small group.

Second, the rate of change of individuals within the populations strongly affects the stability of transmission. Indeed, the differences between the performance of fish in the size = 4 and double replacement conditions, and similarities between the performance of fish in the double replacement and size = 2 conditions, suggest that rate of replacement has a more important effect on transmission stability than absolute population size. Where the number of individuals replaced per trial is a direct function of group size, the rate of loss of information appears to be independent of group size, at least for the range of group sizes considered in this study. Here, the individuals in the trained founding population are replaced at the same proportional rate across different group sizes, resulting in similar opportunity for naïve individuals to learn

socially. After all the founding population have been replaced, the 'cultural relatedness' between a naïve individual and the ancestral population would be approximately the same across group sizes. The group size effects could also be explained by the difference in morphs used in the experiment, as only the calico morph was used in the size = 2 and double replacement conditions. Nevertheless, we consider that this explanation is most unlikely.

DISCUSSION

We have described two transmission chain experiments conducted on laboratory fish that shed light on the factors affecting the stability of socially transmitted information. Both experiments provide evidence that information that is difficult for individual fish to learn asocially can readily be learned socially and can be transmitted along chains of individuals in a population of changing composition. Fish in the experimental conditions, which observed conspecifics solving the feeding tube task, consistently solved the task by themselves. Individual fish were tested over up to 4 days, and typically those in experimental conditions fed repeatedly on consecutive days. However, fish in the control conditions with no such social information rarely or never solved the task. Given Lefebvre & Palameta's (1988) argument that the most compelling evidence for social learning comes from studies in which inexperienced animals are unlikely to learn the target behaviour by themselves, this study provides strong evidence that social learning underlies traditional behaviour in fish, such as migratory behaviour (Helfman & Schultz 1984). As far as we are aware, this is the first study to show the social transmission of information too difficult to learn asocially, in fish.

The studies also shed light on factors affecting the stability of information transmission. Experiment 1 established that a short interruption in the opportunity to perform the transmitted behaviour did not result in an increase in the rate of information loss. Although we cannot rule out the possibility that a more severe disruption would have had a greater adverse effect, taken at face value, our findings suggest that fish traditions may be relatively robust. This conclusion awaits a more comprehensive investigation of the ramifications of disruption to demonstration, but is supported by observations of stable mating site traditions in bluehead wrasse, *Thalassoma bifasciatum* (Warner 1988, 1990). Experiment 2 provides evidence for higher fidelity of information transmission in larger compared to smaller populations. This is largely due to the slower rate of turnover of the larger population, which affords naïve individuals more opportunities to observe experienced conspecifics solving the task and demonstrators greater opportunities to refine their skills, than in smaller populations.

Initially, our findings may appear to conflict with that of Galef & Whiskin (1997) who in a transmission chain study with Norway rats, *R. norvegicus*, found the stability of an experimentally induced food avoidance tradition decreased in fidelity with increased group size. In contrast to our study, where the fish acquire information concerning a single food location, the rat tradition involved the avoidance (or preference) of one of two alternative diets. Thus, in Galef & Whiskin's (1997) study, the slower rate of turnover in a large population afforded naïve individuals more opportunities for trial and error learning of a preference for the alternative 'nontraditional' diet, than in the small population. In our study, there was no alternative option for the fish to learn via asocial learning. This raises the possibility that group size is negatively correlated to transmission fidelity and tradition longevity when the tradition constitutes a preference for one from a set of multiple learned alternative patterns of behaviour (e.g. a binary choice) but positively correlated when the set contains only a single pattern of behaviour (i.e. unary 'choice').

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