

Nine-spined sticklebacks deploy a hill-climbing social learning strategy

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Theoretical models on the adaptive advantages of social learning lead to the conclusion that copying cannot be indiscriminate and that individuals should adopt evolved behavioral strategies that dictate the circumstances under which they copy others and from whom they learn. Strategies that exhibit hill-climbing properties, that would allow a population of individuals to converge on the fitness-maximizing behavior over repeated learning events, are of particular significance due to their potentially critical role in cumulative cultural evolution. Here, we provide experimental evidence that nine-spined sticklebacks (*Pungitius pungitius*) use public information adaptively and in accordance with a hill-climbing social learning strategy. Sticklebacks switch patch preferences to exploit a more profitable food patch if the returns to demonstrator fish are greater than their own but are less likely to copy when low-profitability patches are demonstrated. These findings reinforce the argument that public-information use in nine-spined sticklebacks is an adaptive specialization. More generally, the observation of this sophisticated form of learning in a species of fish supports the view that the presence of enhanced social learning may be predicted better by specific sources of selection than by relatedness to humans. *Key words*: cultural evolution, evolutionary game theory, social learning strategy. [*Behav Ecol* 20:238–244 (2009)]

INTRODUCTION

Numerous animals acquire foraging skills, dietary preferences, mating preferences, or predator evasion tactics or learn calls, songs, or migratory routes, by observing more experienced individuals (Danchin et al. 2004). However, it does not follow that copying others per se is a recipe for success. To the contrary, both evolutionary game theory and population genetic models lead to the prediction that animals ought to be highly selective with respect to the circumstances under which they rely on social learning and the individuals from whom they learn (Boyd and Richerson 1985; Rogers 1988; Giraldeau et al. 2002; Dall et al. 2005). Under intermediate levels of environmental variation, individual fitness is affected by a trade-off in reliance on personal and social information; that is, the costly asocial acquisition of accurate information and the cheap social learning of potentially outdated information (Boyd and Richerson 1985). Consequently, theoretical analyses typically predict a polymorphic equilibrium of asocial and social learning. A history of natural selection in nonhuman animals capable of social learning is also likely to have favored specific adaptive “social learning strategies” that enhance the efficiency of asocial learning by selective or conditional use of both socially and asocially acquired information.

Researchers distinguish between 2 types of social learning strategy (Laland 2004): “when” strategies, which dictate the circumstances under which individuals copy others, and “who” strategies specifying from whom individuals learn. A recent review of nonhuman animals (Kendal et al. 2008) reported good support for several when strategies, including copy-when-asocial-learning-is-costly (Laland and Williams 1998; Coolen et al. 2003; Kendal et al. 2004), copy-when-

uncertain (Rafacz and Templeton 2003; Kendal et al. 2004; van Bergen et al. 2004; Coolen et al. 2005; Galef et al. 2008), and copy-when-dissatisfied (Galef et al. 2008). However, current support for the existence of who strategies is weaker.

One class of social learning strategies of considerable interest are those learning rules that allow individuals to converge on the best (i.e., highest fitness) behavior over repeated iterations. Such “hill-climbing” strategies are important because they potentially support cumulative culture, precipitating a gradual improvement in efficacy or efficiency over time as improvements or elaborations in established behavior spread (a “ratchet effect”; Tomasello 1994). This process is widely thought to have created the wide-ranging and complex culture that we can observe within humans. Schlag (1998, 1999) conducted game theoretical analyses exploring the relative merits of various kinds of “imitation rules,” which revealed a number of alternative social learning strategies with this hill-climbing quality. These include copy-if-better rules, whereby individuals copy others exhibiting behavior patterns that reap greater returns than their own, and various other conditional copying rules, including copying in proportion to the demonstrator's payoff (proportional observation) and copying in proportion to one's dissatisfaction with the payoff to the current behavior (proportional reservation).

Conceivably, the ability to implement a copy-if-better rule requires an appraisal of the payoffs to self and other, together with an ability to compare these, and this ability may not be present in nonhuman animals, whereas other hill-climbing social learning strategies are potentially easier for animals to implement (Laland 2004). However, to date, we know of no unambiguous case of a nonhuman exhibiting either a social learning strategy with this hill-climbing property or cumulative culture, although a tentative case has been made for cumulative culture in the complexity of New Caledonian crows (Hunt and Gray 2003) and chimpanzee nut cracking (Boesch 2003). Were animals to be found that were capable of adopting a hill-climbing social learning strategy it would be of great interest because it would suggest that the species concerned may have an unusually sophisticated social learning capability and raise the possibilities that either cumulative cultural

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evolution may be more prevalent in nonhuman animals than currently believed or that cumulative culture requires more than a hill-climbing strategy to evolve (Laland 2004).

Several recent findings suggest nine-spined sticklebacks as a useful model system in which to explore hill-climbing strategies. Nine-spined sticklebacks are known to be able to exploit public information; that is, they have the ability to judge the relative profitability of food patches solely on the basis of the relative feeding activity of others, without directly assessing patch quality themselves (Coolen et al. 2003). This ability appears to be absent in the closely related three-spined stickleback (*Gasterosteus aculeatus*), even in individuals collected from the same streams as the nine-spined sticklebacks (Coolen et al. 2003). Three-spined sticklebacks were capable of solving a delayed local enhancement task (where, on the basis of prior observation of conspecifics' foraging, they could distinguish between "patches" that do and do not contain food) but failed to solve a public-information use task (where, on the basis of prior observation of conspecifics' foraging, they are required to distinguish between rich and poor food patches). Moreover, nine-spined sticklebacks use public information adaptively; for instance, van Bergen et al. (2004) showed that they will ignore public information if they have reliable, up-to-date personal information yet switch to exploiting public information if their personal information is unreliable or outdated. This suggests that the preference to use social and personal information is not weighted equally; rather, the fish will alternate between the 2 in a conditional manner, according to their respective reliability and cost. Finally, nine-spined sticklebacks will choose the demonstrated rich foraging patch even if more demonstrators are feeding at the demonstrated poor patch (Coolen et al. 2005), establishing that these fish are genuinely able to judge the profitability of patches through observation and are not relying on foraging shoal size as an indirect cue indicative of patch quality.

Here, we test, using an established public-information use of foraging information paradigm (Coolen et al. 2003, 2005; van Bergen et al. 2004), whether nine-spined sticklebacks are able to implement a hill-climbing social learning strategy. The use of this system offers the advantage that we can exploit a previously verified experimental design (Coolen et al. 2003, 2005; van Bergen et al. 2004) to generate data that is directly comparable to both previous experiments and prior theory (e.g., Schlag 1998, 1999). In the experiment, fish were trained that one feeder was rich and the other poor (specifically, that the rich and poor feeders dispensed, on average, 5.11 and 2.89 feeds per session, respectively, during each training round). They were then shown a public demonstration in which the payoffs to demonstrators conflicted with their personal information regarding feeder quality (i.e., the personal-rich feeder became the public-poor feeder, and the personal-poor feeder became "public rich"), before being allowed to choose a feeder at which to forage. During the public demonstration, demonstrators received food at a rate of 2 and 6 feeds per session at the public-poor and public-rich feeders, respectively (henceforth referred to as "2|6"), 4 and 8 feeds (4|8), or zero and 4 feeds (0|4). If fish employ a hill-climbing social learning strategy (either a copy-if-better strategy or a proportional imitation rule), those in the 2|6 and 4|8 conditions should show a preference for the demonstrated rich (better) feeder, whereas those in the 0|4 condition should not copy. (Note, we predict that fish on the 2|6 schedule should copy because their rich demonstrators receive greater reinforcement [6 feeds] than subjects received on average at the personal-rich feeder during training [5.11 feeds]). We expect fish to show less uncertainty in whether or not to copy when faced with unambiguous public information (i.e., those in the 0|4 group).

METHODS

Experimental design

Adult nine-spined sticklebacks were caught using dip nets from Melton Brook, Leicester (52°39'N, 01°06'W), and housed in tanks at the Gatty Marine Laboratory, St Andrews. Water temperature was maintained at 8–12 °C in order to suppress the onset of sexual maturation, and fish were fed to satiation daily on frozen chironomid larvae (bloodworm), except prior to training when test fish were deprived of food for 24 h. Experiments were conducted in an aquarium (30 × 90 cm, 18-cm water level) divided into 3 equal sections with 2 transparent partitions, with a feeder placed at each end of the tank. Feeders consisted of columns (5 × 5 × 35 cm high) with white opaque sides and a transparent front and back (van Bergen et al. 2004; Figure 1). Although both feeders appeared visually similar, after suitable training nine-spined sticklebacks are able to differentiate between them using spatial cues alone (e.g., van Bergen et al. 2004; Coolen et al. 2005). To ensure that objects or events outside the tank would not distract the fish, the outside of 3 sides of the tank was covered with white opaque plastic, and the experimenter observed the tank from within a hide.

The study had 3 experimental conditions and a control. Fish in experimental conditions were given 1) noisy personal information that provided them with the opportunity to feed at 2 feeders and to learn that one was richer than the other (training), 2) a "pretest" to establish that this personal training was effective, 3) conflicting public information, where they observe 2 shoals of conspecific demonstrators feeding at the 2 feeders but with the rich and poor feeders reversed compared with training, and 4) a test to determine their choice of feeder. Accordingly, choice of a feeder is potentially indicative of reliance on either personal or public information. The control condition experienced 1) personal information, 2) pretest, and 4) test, without receiving 3) conflicting public information but instead experiencing a time delay of equivalent duration. The experimental procedures closely follow those outlined in van Bergen et al. (2004).

(i) Personal-information training sessions

Fish were trained in 17 batches of 16 fish each. For each batch, the fish were split into 2 groups of 8 fish, with each group placed in the end sections containing the feeders, separated from an empty central section by transparent partitions (Figure 1). This ensured that each shoal could access only one feeder throughout each 10-min training session although still having visual access to the other feeder. It also prevented the fish from distributing according to the ideal free (or

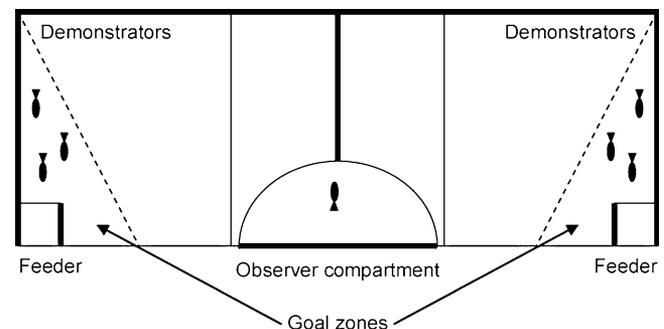


Figure 1

Experimental apparatus for the public demonstration periods. Thick lines represent opaque partitions, thin lines represent transparent partitions, and dashed lines represent goal zone delimitations.

related) distribution, which might have interfered with learning about the relative profitability of the 2 feeders. During 18 training trials (3 per day for 6 days), both groups experienced 9 feeding sessions at each of 2 feeders. One feeder was designated “rich” and the other “poor” at random, and this designation was maintained throughout training. During training, fish received noisy personal information that, in 78% of the trials (7 of the 9 sessions), the rich feeder provided food at 3 times the rate of the poor feeder, such that the rich feeder provided 3 bloodworms 6 times in 10 min (every 90 s), whereas poor feeders delivered 3 bloodworms twice in 10 min (at 1 min 30 s and 6 min). In the remaining sessions, the feeding rate at rich and poor feeders was reversed, so that the average delivery rate at the rich and poor feeders (labeled “personal rich” and “personal poor”) during training was 5.11 and 2.89 bloodworm deliveries per trial, respectively. At these specific parameter values, and with 6 versus 2 food deliveries to rich and poor feeder, respectively, during the public demonstration, van Bergen et al. (2004) determined that nine-spined sticklebacks weight personal and public information equally. These values were chosen to minimize the probability of ceiling or floor effects at test. When bloodworms were delivered at the rich feeder but not at the poor feeder, water in which bloodworms had been defrosted was delivered at the poor feeder in an attempt to control for residual odor cues. To reduce exploratory behavior during testing, each group was left in the experimental tank overnight after the last day of personal training, so that the fish were familiar with the tank devoid of partitions. Feeders were not present during this time, and they received no food after the final training trial in order to increase motivation during the test phase. Parts (ii), (iii), and (iv) of the experiment all took place on the day after the completion of training (day 7).

(ii) *Preference test after personal-information training*

Fish were pretested individually for a feeder preference to determine whether they had learned which feeder was rich. Each fish was placed in the central section of the experimental tank, with opaque partitions on either side, to acclimatize for 5 min. The test started when the partitions were removed, revealing the feeders in the same locations as during the personal-information training sessions, but no food was provided. The location of the focal fish was recorded every 6 s for 5 min. A fish was deemed to be in a goal zone if its head and body, up to the pectoral fins, were inside the goal perimeter. Any fish exhibiting freezing behavior or moving around the tank quickly and erratically were removed from the experiment as were fish that did not enter either goal zone within 5 min. Only subjects showing a preference for the rich feeder were used further.

(iii) *Public demonstration*

Those fish in the experimental conditions that successfully chose the rich feeder then experienced a public demonstration that conflicted with their personal information. In this demonstration, the rich feeder (or public-rich feeder) was that which had been poor for the majority of that group’s personal training sessions. A focal fish (the observer) was placed in a semicircular transparent compartment in the middle of the experimental tank, and partitions were placed as shown in Figure 1. Two groups of demonstrators, each consisting of 3 fish, were placed in the end sections of the tank. Two opaque partitions were placed alongside the transparent partitions, hiding the feeders and demonstrators from the observer. The demonstration began when the opaque partitions were removed and lasted 10 min. The feeders had opaque sides facing the observer and transparent fronts facing the demonstrators, who would peck at the bloodworms as they sank to the bottom of the feeder where they were eaten

through a slot. Observers could not see the food directly but could use the demonstrators’ foraging activity to determine the profitability of each feeder. Nine-spined sticklebacks are known to be able to choose the rich feeder after a single public demonstration (Coolen et al. 2003).

Three experimental conditions varied according to the patterns of food delivery to the 2 shoals during the public demonstration, with poor and rich demonstrator shoals receiving 4 versus 8 (i.e., 3 bloodworms 4 times in 10 min to the poor feeder vs. 3 bloodworms 8 times in 10 min to the rich feeder; 4|8), 2 versus 6 (2|6), or zero versus 4 (0|4) food deliveries during the demonstration. The control subjects received no public demonstration, and visual access to the feeders was prevented by opaque partitions. Control subjects experienced a delay of equivalent duration within the semicircular compartment.

Again, when bloodworms were delivered at the rich feeder but not at the poor feeder, water in which bloodworms had been defrosted was delivered at the poor feeder. In order to investigate the possibility of residual olfactory cues biasing the findings, van Bergen (2004) tested whether sticklebacks subjected to an identical procedure but contained in an opaque compartment during public demonstration showed a preference for the public-rich feeder; at test no such preference was observed. This suggests that residual odor cues are unlikely to explain any preferences manifest in our data.

(iv) *Preference test after public demonstration*

After the public demonstration, opaque partitions were replaced at either side of the central compartment, the demonstrators and any remaining worms were removed from the experimental tank, and the observer was released from its compartment and allowed to swim around the central section of the tank for 5 min. All partitions were then removed, and the location of the observer was recorded every 6 s from when the observer left the central section until 90 s after it entered a goal zone (see Figure 1). No food was provided during the preference test. Our analysis focuses on the behavior of the fish during this choice test.

Analysis

In order to assess whether fish were using information gained during the public demonstration or their own personal information about the quality of a feeder, we quantified 2 measures of feeder preference: 1) *first feeder choice* was the identity (i.e., public rich or public poor) of the first feeder to which each fish swam and 2) *relative feeder preference* was the relative difference (public rich minus public poor) in the number of instances that the fish was present at each feeder, from instantaneous sampling of the fish’s location every 6 s for the first 90 s after the start of the choice test. We also tested whether the salience of the demonstrated cue, and thus the uncertainty of feeder choice, was related to the difference in payoff between the 2 feeders during demonstration, using 2 measures of feeder preference uncertainty: 1) *time to approach any feeder* was the time (to the nearest 6 s from instantaneous sampling) that it took the focal fish to initially approach either the rich or the poor feeder and 2) *number of feeder switches* was the number of times the focal fish moved between feeders during the 90 s after the start of the choice test.

As a result of constraints on the number of fish, some fish that were trained but were not used in any of the 4 treatments (i.e., they did not exhibit a preference for the personal-rich feeder in the first choice test) were reused in a later batch. We incorporated this as a fixed variable, referred to as the number of “exposures” to personal training, and found that this variable did not affect the results. During the experiment,

the location (or “end”) of the personal-rich and personal-poor feeders was counterbalanced across batches (i.e., groups of trained fish), and our statistical models assume random effects of batch (i.e., the batch of 8 fish in which an individual was trained). Where linear mixed models were used, residuals were tested for normality using Shapiro’s test and homogeneity was tested using Bartlett’s test. Generalized linear mixed models were used for measures with nontransformed nonnormal error structures. Orthogonal Helmert contrasts were used to test hypotheses. The effect of a hill-climbing strategy on feeder preference was tested using a vector of treatment levels ordered by the expected preference for the personal-poor feeder (control, 0|4, 2|6, 4|8); the effect of public information (at the public-rich feeder) on feeder preference was tested by contrasting experimental treatments against controls, using the treatment level vector (0|4, 2|6, 4|8, control); and the effect of relative difference in payoff between public- and personal-rich feeders on preference uncertainty was tested using the treatment level vector (0|4, 2|6, 4|8).

RESULTS

Feeder preference

Controls

Fish in the control group ($n = 25$), that received no public demonstration, showed a significant preference for the personal-rich feeder in terms of both their first feeder choice (chi-square test: $\chi^2 = 6.76$, degrees of freedom [df] = 1, $P = 0.009$; Figure 2a) and relative feeder preference (1-sample t -test: $t = -3.38$, df = 24, $P = 0.002$; Figure 2b), confirming that personal training resulted in a preference for the personal-rich feeder.

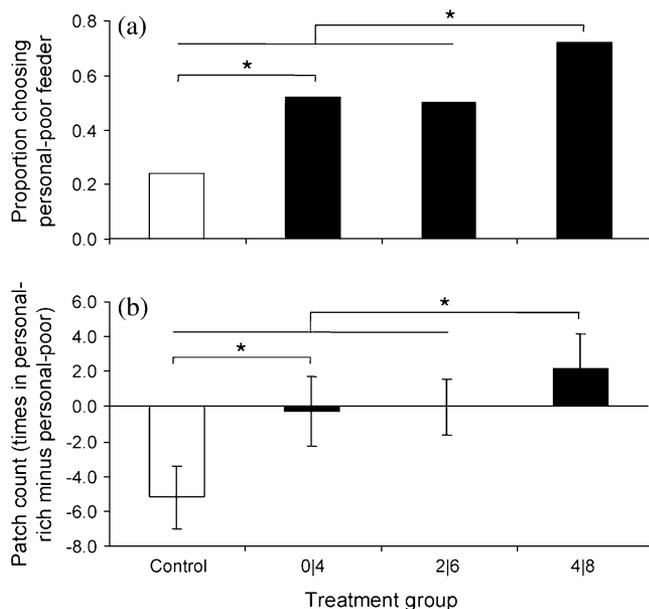


Figure 2
(a) Proportion of fish choosing the personal-poor feeder (subsequently the public-rich feeder) and (b) mean \pm standard error difference (public rich minus public poor) in the number of instances that the fish visited each feeder, from instantaneous sampling of the fish’s location every 6 s for the first 90 s after the start of the choice test, in control (no public demonstration; white bars), 0|4 (i.e., 0 and 4 deliveries to poor and rich feeders, respectively, during the public demonstration), and 2|6 and 4|8 groups (see text for full details). Horizontal lines denote significant differences between groups; * $P < 0.05$.

First feeder choice

Fish in the 4|8 treatment significantly preferred to swim first to the public-rich feeder ($\chi^2 = 4.84$, df = 1, $n = 25$, $P = 0.028$; Figure 2a). In contrast, neither of the other treatments differed significantly from chance (0|4: $\chi^2 = 0.04$, df = 1, $n = 25$, $P = 0.8415$; 2|6: $\chi^2 = 0$, df = 1, $n = 26$, $P = 1$). We compared the first feeder choice across treatments by fitting a generalized linear mixed model with a binomial error structure and Helmert contrasts. The minimal adequate model included significant contrasts comparing controls against 0|4 ($z = 2.27$, $n = 101$, $P = 0.024$) and comparing controls, 0|4, and 2|6 against 4|8 ($z = 2.49$, $n = 101$, $P = 0.013$), consistent with implementation of a copy-if-better strategy. A separate contrast analysis found a significant contrast comparing 0|4, 2|6, and 4|8 against controls ($z = -3.11$, $n = 101$, $P = 0.002$), suggesting that public demonstration enhanced the mean preference for the public-rich feeder over the personal-rich feeder. The observation that the 0|4 group chose the public-rich feeder more often than the controls provides some support for a copy-if-unambiguous or always-copy strategy being deployed in this group.

Relative feeder preference

First, we examined whether each of the test treatments exhibited a feeder preference. During the first 90 s, fish in the 4|8 treatment showed a significant preference for the public-rich feeder (Wilcoxon signed-rank test: $V = 187.5$, $n = 25$, $P = 0.049$; Figure 2b). Neither of the other 2 test treatments exhibited a feeder preference (0|4: $V = 148$, $n = 25$, $P = 0.966$; 2|6: $V = 111.5$, $n = 26$, $P = 0.903$). Next, we compared feeder count measures across all treatments. A full linear mixed model was fit to the data with Helmert contrasts. The minimum adequate model included significant contrasts comparing controls against 0|4 ($t = 2.43$, df = 81, $P = 0.017$) and comparing controls, 0|4, and 2|6 against 4|8 ($t = 2.27$, df = 81, $P = 0.026$). The contrast comparing controls and 0|4 against 2|6 revealed a nonsignificant trend ($t = 1.73$, df = 81, $P = 0.087$). Finally, a minimum adequate linear mixed model gave a significant Helmert contrast comparing 0|4, 2|6, and 4|8 against controls ($t = -3.56$, df = 81, $P = 0.001$), suggesting that public demonstration enhanced the mean preference for the public-rich feeder over the personal-rich feeder. These findings provide support for a hill-climbing strategy.

Uncertainty measures

Time to approach any feeder

A linear mixed model with a log-transformed response variable and Helmert contrasts revealed one significant contrast, comparing 0|4 against 2|6 ($t = 2.62$, df = 57, $P = 0.011$; 0|4 and 2|6 against 4|8, $t = -0.40$, df = 57, $P = 0.687$; Figure 3a). Thus, fish in the 2|6 condition took significantly longer than fish in the 0|4 condition to approach a feeder. A similar model, but using treatment contrasts, found that control fish took significantly longer to approach a feeder than those in the 0|4 group ($t = 2.75$, df = 81, $P = 0.004$; Figure 3a), but not 2|6 or 4|8 (both $P > 0.13$).

Number of feeder switches

We fit a linear mixed model with Helmert contrasts to the log-transformed number of feeder switches and found one significant contrast, comparing 0|4 against 2|6 ($t = 2.72$, df = 52, $P = 0.009$; 0|4 and 2|6 against 4|8, $t = -0.31$, df = 52, $P = 0.379$; Figure 3b). Thus, fish in the 2|6 condition exhibited more switches between feeders than fish in the 0|4 condition. Control fish switched feeders significantly more

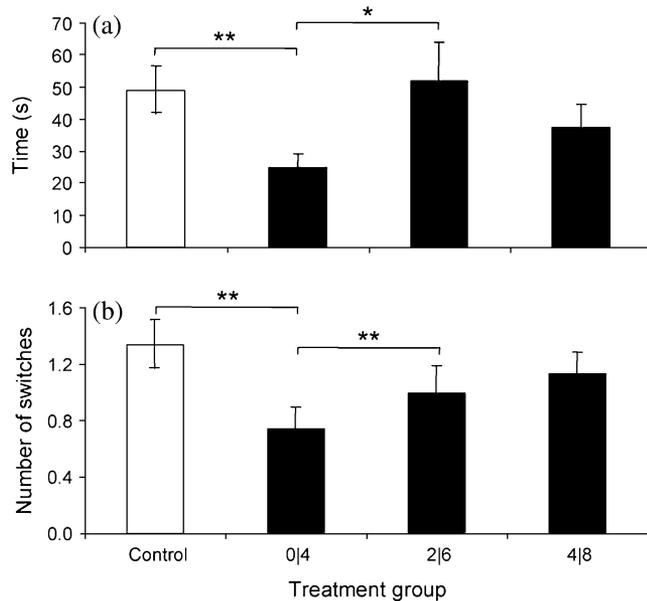


Figure 3
 (a) Mean \pm standard error time to approach the first feeder and (b) number of feeder switches during the 90 s after first feeder choice in control (white bars), 0|4, 2|6, and 4|8 groups (see text for full details). Horizontal lines denote significant differences between groups; * $P < 0.05$, ** $P < 0.01$.

frequently than those in the 0|4 group ($t = 2.59$, $df = 76$, $P = 0.006$; Figure 3a) but not 2|6 or 4|8 (both $P > 0.19$).

DISCUSSION

The results of this study provide experimental evidence that nine-spined sticklebacks are able to utilize public information efficiently, switching patch preferences to exploit a more profitable food patch if the returns to demonstrator fish are greater than the returns expected from previous personal experience but ignoring public information when low-profitability patches are demonstrated. Overall, the measures of first feeder choice and relative feeder preference indicate that the sticklebacks are deploying a hill-climbing social learning strategy, consistent with the implementation of a copy-if-better or proportional imitation rule (Schlag 1998, 1999; Laland 2004). The term copy-if-better is consistent with an array of possible strategies specifying the degree of copying (Schlag 1998). For instance, an “absolute” implementation would predict equal rates of copying in 2|6 and 4|8 conditions, whereas a “proportional” implementation would predict greater copying in the 4|8 than the 2|6 condition (Schlag 1998; Laland 2004). Conversely, if experimental subjects were to always copy, or if they merely learned that there was a conflict between public and personal information, or if their rate of copying depended only on their satisfaction with their personal information, then there would be no difference between experimental conditions in the frequency of copying. Moreover, if fish were pursuing a copy-if-unambiguous strategy, whereby they copied the demonstrators’ behavior whenever they received a clear and distinct social cue, then fish would have copied more in the 0|4 group than 2|6 than 4|8 because the clarity of the public demonstration followed this pattern.

In this experiment, fish exhibited a strong preference for the public-rich feeder when the quality of this feeder was demonstrated to be high relative to the quality of the personal-rich feeder (i.e., treatment 4|8). Moreover, fish in the 4|8 treatment

exhibited more copying than treatments with lower relative public versus personal-rich feeder payoff (2|6, 0|4, and controls), consistent with a proportional, but not absolute, implementation of copy-if-better. Finally, all experimental groups chose the public-rich feeder more frequently than the controls, suggesting that some degree of copying had taken place in the 0|4 condition. These patterns would not be expected if fish ignored social information, in which case the conditions would not differ. Nor would the pattern of results be generated if fish were solely paying attention to public (and not personal) information concerning the *relative* payoffs during demonstration as the ratio of public-rich to public-poor payoffs are 0|4 $>$ 2|6 $>$ 4|8. Finally, these differences would not be expected if fish were only paying attention to the absolute difference in the public-information feeder quality as this remains constant across treatments (i.e., $4 - 0 = 6 - 2 = 8 - 4 = 4$).

Although none of the considered strategies can explain our findings alone, a hill-climbing strategy (either a copy-if-better or proportional observation rule), combined either with a weak deployment of an always-copy strategy across all conditions or with the weak deployment of a copy-if-unambiguous strategy in the 0|4 condition alone, could account for the data. However, there is unambiguous support in the data for the deployment of one of these hill-climbing algorithms.

The copy-if-better strategy predicts that fish in the 0|4 treatment would not copy the demonstrators. Interestingly, fish in the 0|4 treatment appear to exhibit an absence of feeder preference, similar to those in the 2|6 treatment (in 2|6, this effect replicates findings by van Bergen et al. 2004). Here analyses of the uncertainty measures provide clues to the strategies adopted by the fishes in these 2 conditions. Fish in the 0|4 treatment exhibit little evidence of uncertainty, as witnessed by their rapid decision making and small number of feeder switches. One possible explanation for the absence of a preference in this condition is that approximately half of the fish rely primarily on their personal information and the other half on the unambiguous social information. Conversely, we see evidence for far more uncertainty among fish in the 2|6 treatment, perhaps suggesting that fish in this condition processed both kinds of information and were hampered in their decision making by its conflicting character. The observation that there are differences in the degree of uncertainty between 0|4 and 2|6 conditions mitigates against an explanation for their similar levels of copying in terms of an identical process, such as weak deployment of always-copy. Rather, the greater than expected level of copying in the 0|4 group seems to result from a process operating solely in this group. The most plausible explanation is that the saliency of an unambiguous “social signal” that occurs when food is only observed at one of the 2 feeders leads to some copying. Interestingly, there were also high levels of apparent uncertainty in the control fish. It is possible that the increased time taken to make their first feeder choice might be because sticklebacks are a social species, and the perception of being alone in the tank (in contrast to experimental fish that had recently observed conspecifics foraging) was stressful for them, whereas the high number of feeder switches may be caused by their certainty of feeder quality (they received no conflicting public demonstration) being undermined by the lack of food available during the test.

Although the elevated rate of copying in the 4|8 relative to the 2|6 condition implies a proportional rather than absolute implementation of a hill-climbing strategy, it is not clear which proportional rule is being deployed. Schlag (1998) distinguished between a proportional observation rule, which merely requires subjects to copy the behavior of the demonstrator with a probability proportional to the demonstrator’s

payoff, and a proportional imitation rule, which requires subjects to copy in proportion to the difference between the demonstrator's and their own payoff. A further experiment that manipulated the payoff associated with personal information would clarify this situation. It also remains to be established to what extent the fish are sensitive to the relative payoffs of the 2 demonstrated feeders, as opposed to the absolute payoff at the demonstrated rich feeder. Would for instance, fish behave differently if exposed to 4|8 and 0|8 conditions? The findings of this experiment suggest such a difference may occur because fish exposed to 0|8 might be influenced by both copy-if-better and copy-if-unambiguous strategies.

Recent human culture is characterized by the ratchet effect (Tomasello 1994) or an increase in the complexity or efficiency of technology over time (Enquist and Ghirlanda 2007). There is little direct evidence within animal populations of additive, incremental improvement in behavior or technological advance, which has led to the argument that certain key psychological abilities are critical to cumulative evolution. Capacities for teaching and imitation have been widely touted as likely candidate processes (Boyd and Richerson 1985; Galef 1992; Tomasello 1994), but recent evidence for imitation (now observed in 5 species of mammal discounting humans and 6 species of birds; Hoppitt and Laland 2008) and teaching (observed in meerkats and ants; Franks and Richardson 2006; Thornton and McAuliffe 2006) in animals undermines this argument. Schlag's (1998) theoretical findings suggest another possibility. Intrinsic to ratcheting is the deployment of a social learning strategy with this hill-climbing property capable of taking populations to the fitness-maximizing behavior. It is thus possible that many animal species rarely exhibit ratcheting because individuals are unable to ascertain with sufficient reliability whether the behaviors of another individual are more profitable than their own or are unable to make a judgment as to how much better the alternative is. Alternatively, animals may not exhibit other social learning strategies with this hill-climbing property that are not reliant on such comparisons between payoff to self and other. Our results, however, suggest that nine-spined sticklebacks provide a clear example of a nonhuman capable of a ratcheting social learning strategy.

The use of a sophisticated social learning strategy by nine-spined sticklebacks reinforces the argument that such strategies constitute an adaptive specialization (Laland 2004). Coolen et al. (2003) examined the propensity of three-spined (*G. aculeatus*) and nine-spined sticklebacks to exploit public information. Nine-spined sticklebacks preferentially chose the feeder that had been demonstrated to be rich, suggesting that they were able to exploit public information. However, three-spined sticklebacks appeared reluctant or unable to use prior public information and swam with equal frequency to rich and poor feeders, a finding confirmed by Webster and Hart (2006) in a study involving the acquisition of subhabitat preferences. Moreover, nine-spined, but not three-spined, sticklebacks utilized vegetative cover during demonstration periods (Coolen et al. 2003). The collection of personal information in open water is costlier for nine-spined sticklebacks because they have inferior structural antipredator defenses and are consumed preferentially over three-spined sticklebacks by piscivorous fish (Hoogland et al. 1957). Because of these costs, nine-spined sticklebacks may forego the opportunity to collect reliable personal information and favor vicarious assessment of foraging opportunities through observational learning, perhaps utilizing the copy-if-better strategy that theory has been established to be highly efficient (Schlag 1998). Thus public-information use in sticklebacks may be regarded as an adaptive specialization in learning, reflecting the differential costs

of personal-information acquisition. Allied with observations of advanced cognition, including sophisticated forms of social learning, in parrots and cetaceans (Pepperberg 1990; Rendell and Whitehead 2001; Heyes and Saggerson 2002), our findings support the view that enhanced social learning may be a manifestation of convergent selection for cognitive capabilities in distant taxa, rather than predicted by relatedness to humans.

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REFERENCES

- Boesch C. 2003. Is culture a golden barrier between human and chimpanzee? *Evol Anthropol.* 12:82–91.
- Boyd R, Richerson PJ. 1985. *Culture and the evolutionary process.* Chicago: Chicago University Press.
- Coolen I, Day RL, Laland KN. 2003. Species differences in adaptive use of public information in sticklebacks. *Proc Biol Sci.* 270:2413–2419.
- Coolen I, Ward AJW, Hart P, Laland KN. 2005. Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. *Behav Ecol.* 16:865–870.
- Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW. 2005. Information and its use by animals in evolutionary ecology. *Trends Ecol Evol.* 20:187–193.
- Danchin E, Giraldeau LA, Valone TJ, Wagner RH. 2004. Public information: from nosy neighbors to cultural evolution. *Science.* 305:487–491.
- Enquist M, Ghirlanda S. 2007. Evolution of social learning does not explain the origin of human cumulative culture. *J Theor Biol.* 246:129–135.
- Franks NR, Richardson T. 2006. Teaching in tandem-running ants. *Nature.* 439:153.
- Galef BG. 1992. The question of animal culture. *Hum Nat.* 3:157–178.
- Galef BG, Dudley KE, Whiskin EE. 2008. Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. *Anim Behav.* 75:631–637.
- Giraldeau L-A, Valone TJ, Templeton JJ. 2002. Potential disadvantages of using socially acquired information. *Philos Trans R Soc Lond B Biol Sci.* 357:1559–1566.
- Heyes CM, Saggerson A. 2002. Testing for imitative and non-imitative social learning in the budgerigar using a two-object/two-action test. *Anim Behav.* 64:851–859.
- Hoogland R, Morris D, Tinbergen N. 1957. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defence against predators (*Perca* and *Esox*). *Behaviour.* 10:205–216.
- Hoppitt W, Laland KN. 2008. Social processes influence learning in animals: a review of the evidence. *Adv Study Behav.* 38:105–165.
- Hunt GR, Gray RD. 2003. Diversification and cumulative evolution in tool manufacture by New Caledonian crows. *Proc Biol Sci.* 270:867–874.
- Kendal RL, Coolen I, Laland KN. 2004. The role of conformity in foraging when personal and social information conflict. *Behav Ecol.* 15:269–277.
- Kendal RL, Coolen I, Laland KN. 2008. Adaptive trade-offs in the use of social and personal information. In: Dukas R, Ratcliffe JM, editors. *Cognitive ecology: the evolutionary ecology of learning, memory and information use.* Chicago: University of Chicago Press.
- Laland KN, Williams K. 1998. Social transmission of maladaptive information in the guppy. *Behav Ecol.* 9:493–499.
- Laland KN. 2004. Social learning strategies. *Learn Behav.* 32:4–14.
- Pepperberg I. 1990. Cognition in an African grey parrot (*Psittacus erithacus*): further evidence for comprehension of categories and labels. *J Comp Psychol.* 104:41–52.
- Rafacz M, Templeton JJ. 2003. Environmental unpredictability and the value of social information for foraging starlings. *Ethology.* 109:951–960.
- Rendell L, Whitehead H. 2001. Cetacean culture: still afloat after the first naval engagement of the culture wars. *Behav Brain Sci.* 24:309–324.

- Rogers AR. 1988. Does biology constrain culture? *Am Anthropol.* 90:819–831.
- Schlag K. 1998. Why imitate, and if so, how? *J Econ Theory.* 78:130–156.
- Schlag K. 1999. Which one should I imitate? *J Math Econ.* 31:493–522.
- Thornton A, McAuliffe K. 2006. Teaching in wild meerkats. *Science.* 313:227–229.
- Tomasello M. 1994. The question of chimpanzee culture. In: Wrangham R, McGrew W, de Waal F, Heltne P, editors. *Chimpanzee cultures.* Cambridge (MA): Harvard University Press. p. 301–317.
- van Bergen Y. 2004. An investigation into the adaptive use of social and asocial information [PhD thesis]. [Cambridge]: University of Cambridge.
- van Bergen Y, Coolen I, Laland KN. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proc Biol Sci.* 271:957–962.
- Webster MM, Hart PJB. 2006. Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. *Behav Ecol Sociobiol.* 60:77–86.