

Learning by proportional observation in a species of fish

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Theoretical analyses predict that animals should not copy other individuals indiscriminately but rather should do so selectively, according to evolved behavioral strategies that dictate the circumstances under which they copy. Here, we show experimentally that nine-spined sticklebacks (*Pungitius pungitius*) use social information in accordance with 1 of 3 theoretically predicted optimal strategies to guide their foraging behavior. Under test, sticklebacks copied the foraging patch choice of demonstrator individuals with a probability proportional to the demonstrators' payoff. The observation of this highly efficient form of learning in a species of fish supports the view that the presence of enhanced social learning may be better predicted by specific sources of selection than by how closely the species is related to humans and sheds light on the character of an adaptive specialization in stickleback learning. *Key words*: evolutionary game theory, nine-spined stickleback, social learning strategy. [*Behav Ecol*]

Although countless animals learn life skills, such as what to eat or how to evade predators, by observing more experienced individuals (Laland 2008), it does not follow that copying others per se is a recipe for success. Evolutionary game theory and population genetic models predict that animals should be highly selective about when they copy others and when they rely on their own experience (Boyd and Richerson 1985; Rogers 1998; Giraldeau et al. 2002). Such models find that a balance of asocial and social learning is optimal and predict that individuals will exploit social information conditionally, according to evolved rules, termed "social learning strategies" (Laland 2004).

In a theoretical analysis designed with humans in mind, economist Karl Schlag used game theory models to compare the efficacy of a number of such social learning strategies, reporting considerable variation in the efficiency of alternative rules (Schlag 1998). For instance, when information concerning the success of others is unreliable and noisy, copying others who reap returns greater than the observer is more efficient than copying the most successful observed behavior. However, always copying individuals who seem to be reaping greater returns can lead the entire population to choose the alternative with the lowest expected payoff. Schlag (1998) identified 3 equally efficient solutions to this paradox in the form of 3 optimal social learning strategies that each takes populations to the fitness-maximizing behavior (see also Schlag 1999; Apesteguia et al. 2007):

1. The first solution (which Schlag termed "proportional observation") requires individuals to copy the behavior of a demonstrator with a probability proportional to the demonstrator's payoff.
2. The second solution (which Schlag called "proportional reservation") requires the individual to retain its current

(personal) behavior with a probability equal to its satisfaction, which is linearly related to the size of the payoff to its current behavior. This strategy does not require individuals to assess the payoff to a demonstrator or to make any judgments as to the relative profitability of alternative behavior patterns.

3. The third solution (which Schlag called "proportional imitation") combines rules 1 and 2, so that observers copy a demonstrator with a probability proportional to how much better that individual performed than them.

These 3 alternatives therefore refer to cases where the likelihood of copying is a function of the payoff to the demonstrator, payoff to self, and difference between these, respectively. Analysis by Schlag (1998) established that if individuals were to adopt these learning rules, then the population would rapidly converge on the behavior with the highest payoff (and would continue to track the fitness maximizing behavior in a noisy and changeable environment). These rules are far more effective than individual learning because individuals pool their knowledge and more effective than alternative social learning rules, which do not necessarily lead individuals to the optimal behavior.

We have recently shown that nine-spined sticklebacks (*Pungitius pungitius*) can assess the quality of food patches solely by monitoring the success or failure of others to obtain food (Coolen et al. 2003, 2005), that they will differentially base their patch-choice decisions on personal and/or social information depending on the relative quality of these sources (van Bergen et al. 2004), and that they are able to switch foraging 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 (Kendal et al. 2009). These results are consistent with the fish employing a proportional (rather than absolute) implementation of a "copy-if-better" social learning strategy (Laland 2004); however, the results are ambiguous as to which rule (proportional observation, reservation, or imitation; Schlag 1998, 1999) is being deployed. Here, we extend this work by presenting an experiment that allows us to differentiate between these alternatives using an established public information use of foraging information

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Table 1

Training regimes and predicted levels of copying for each of the 3 learning rules “proportional observation,” “proportional reservation,” and “proportional imitation.” During the experiment, fish were given the opportunity to feed at 2 feeders and to learn that one was richer than the other (personal training). Fish in the experimental conditions then experienced conflicting public information, where they observed 2 shoals of conspecific demonstrators feeding at the 2 feeders, but with the rich and poor feeders reversed compared with training (demonstration); control fish did not receive conflicting public information but instead experienced a time delay of equivalent duration. See text for full details

	Control 1	6 2 then 2 6	6 2 then 4 8	Control 2	8 4 then 2 6	8 4 then 4 8
Training regime						
Personal training	6 2 feeding schedule ^a	6 2 feeding schedule	6 2 feeding schedule	8 4 feeding schedule	8 4 feeding schedule	8 4 feeding schedule
Demonstration	None	2 6 feeding schedule	4 8 feeding schedule	None	2 6 feeding schedule	4 8 feeding schedule
Predicted levels of copying						
Proportional observation	Low	Intermediate	High	Low	Intermediate	High
Proportional reservation	Low	High	High	Low	Intermediate	Intermediate
Proportional imitation	Low	Intermediate	High	Low	Low	Intermediate

^a A 6|2 feeding schedule refers to 6 and 2 food deliveries per 10 min trial at the rich and poor feeders, respectively.

paradigm (Coolen et al. 2003, 2005; van Bergen et al. 2004; Kendal et al. 2009). Specifically, we evaluate the qualitative predictions of analyses by Schlag (1998, 1999), exploring whether nine-spined sticklebacks behave in a manner consistent with the deployment of his optimally efficient rules or whether they utilize alternative learning strategies. Theoretical work by Schlag (1998, 1999) lends itself well to qualitative tests because each of his 3 highly efficient social learning rules make quite distinctive qualitative predictions, a summary of which are given in Table 1.

MATERIALS AND METHODS

Study species

Several findings highlight nine-spined sticklebacks as a useful model system in which to address social learning strategies. First, there is strong evidence that these fish are capable of learning by observing the behavior of others. Nine-spined sticklebacks have been found to gage the relative profitability of food patches through observing the relative feeding activity of others without directly sampling patch quality themselves (Coolen et al. 2003, 2005; van Bergen et al. 2004; Kendal et al. 2009), a form of social learning known as “public information use.” Second, 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), a species difference that we have found to be robust despite collecting fishes from more than 20 populations around the United Kingdom (Webster MM, Laland KN, unpublished data). This supports the argument that public information use in nine-spined sticklebacks is an adaptive specialization rather than a general learning ability and that the manner in which these fish learn has been fine-tuned by natural selection to enhance foraging in this species. Third, nine-spined sticklebacks do not copy conspecifics indiscriminately but switch between utilizing social and asocial sources of information in an adaptive manner: For instance, they will ignore social cues if they have reliable up-to-date personal information, yet switch to exploiting public information if their personal information is unreliable or outdated (van Bergen et al. 2004). Hence, these fish are deploying a more sophisticated strategy than simply always copying the best available option. Fourth, the results of previous studies confirm the aforementioned findings and rule out alternative explanations, suggest-

ing that the interpretations are robust and the experimental procedures provide a reliable means of testing for social information use (Coolen et al. 2003, 2005; van Bergen et al. 2004; Kendal et al. 2009). For instance, nine-spined sticklebacks choose the demonstrated rich 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 nor are they reliant on residual olfactory cues or other biases (Coolen et al. 2003, 2005; van Bergen et al. 2004).

Subjects and apparatus

Adult nine-spined sticklebacks were caught using dip nets from Melton Brook, Leicester (lat 52°39'N, long 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; any fish showing signs of sexual maturation were not included in the experiment. Fish were fed 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 sections with 2 transparent partitions, with a feeder placed at each end of the tank (Figure 1). Feeders consisted of columns (5 × 5 × 35-cm

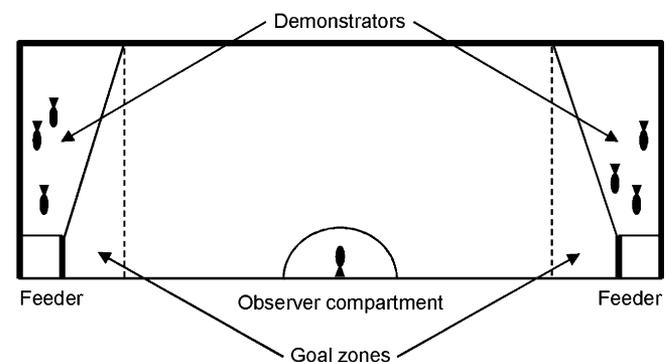


Figure 1 Experimental apparatus for the public demonstration periods. Thick lines represent opaque partitions, thin lines represent transparent partitions, and dashed lines represent goal zone delimitations.

high) with opaque sides and a transparent front (van Bergen et al. 2004). To facilitate learning, 1 feeder was colored blue and the other yellow (Girvin and Braithwaite 1998), although which color of feeder was designated “rich” or “poor” (see below) was balanced within experimental groups. A pilot experiment confirmed that fish showed no prior preference for either color of feeder (binomial test: $n = 20$, $P = 0.82$). To ensure that objects or events outside the tank would not distract the fish, the outsides of 3 sides of the tank were covered with opaque black plastic and the experimenter observed the tank from within a hide.

Experimental procedure

Adult nine-spined sticklebacks were allocated to 1 of 4 experimental or 2 control conditions. Fish in experimental conditions were given (i) noisy personal information which provided them with the opportunity to feed at 2 feeders and to learn that 1 was richer than the other (training); (ii) a “pretest” to establish that this personal training was effective; (iii) conflicting public information, where they observed 2 shoals of conspecific demonstrators feeding at the 2 feeders but with the rich and poor feeders reversed compared with training; and (iv) a test, to determine their final choice of feeder. Accordingly, choice of a feeder is potentially indicative of reliance on either personal or public information. The control conditions experienced (i) personal information, (ii) pretest, and (iv) test, without receiving (iii) conflicting public information but instead experiencing a time delay of equivalent duration. A summary of the procedures for the 6 conditions and predictions for the expected level of copying across these conditions made by the aforementioned learning rules are given in Table 1. Full details of the experimental procedures are given below.

Personal information training sessions

Fish were trained in groups of 16. For each group, the fish were split into 2 batches of 8 fish, with each batch 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 1 feeder throughout each training session, although still having visual access to the other feeder. It also prevented the fish from distributing according to the ideal free (or related) distribution, which might have interfered with learning about the relative profitability of the 2 feeders. Over 16 training trials (4 per day for 4 days), both batches experienced 8 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. For half the experimental fish, the rich feeder provided food (3 small bloodworms) 6 times during each 10 min training session (every 90 s), whereas poor feeders delivered bloodworm twice in 10 min (at 90 s and 6 min), hereafter referred to as a “6|2” feeding schedule. The other half received food 8 times in 10 min at the rich feeder and 4 times in 10 min at the poor feeder (at 90 s and then every 65 or 130 s thereafter, respectively) (i.e., an “8|4” schedule). 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. Noise was introduced into the training procedure by switching the rate of food delivery to the “rich” and “poor” feeders in 25% of the trials. Van Bergen et al. (2004) determined that at similar noise levels to this nine-spined sticklebacks weight personal and public information equally, and so this minimized the probability of ceiling or floor effects at

test. To reduce stress, each group was left in the experimental tank between training sessions, so that the fish were familiar with the tank. Feeders were not present during this time, and fish were confined to the central third by transparent partitions, with each batch separated by a diagonal transparent divider. Fish received no food after the final training trial in order to increase motivation during the subsequent test phase. Parts (ii), (iii), and (iv) of the experiment all took place on the day after the completion of training (day 5).

Preference test after personal information training

The day following the completion of training, fish were pretested individually for a feeder preference to determine whether they had learned which feeder was “rich.” Each focal fish was placed in a semicircular transparent compartment in the middle of the experimental tank (Figure 1) and allowed to acclimatize for 2 min. Feeders were present in the same locations as during the personal information training sessions, but no food was provided. The test started when the transparent compartment was removed, and the time taken for the fish to enter a goal zone (10 cm at the end of each tank encompassing a feeder; Figure 1) was recorded; 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. Altogether 66% of fish (120/181, binomial test: $P < 0.001$) showed a preference for the rich feeder during this test.

Public demonstration

Those fish in the experimental conditions that successfully chose the personal-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 designated “poor” for that group’s personal training sessions. A focal fish (the observer) was placed in the 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 size-matched conspecifics, were placed in the end sections of the tank, and the focal fish experienced a public demonstration lasting 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. 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, Coolen et al. (2005) 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. Moreover, as food or water was delivered to both feeders simultaneously, the fish were unable to use cues from the experimenter’s movements to inform their decision making. Nine-spined sticklebacks are known to be able to choose the “rich” feeder after a single public demonstration (Coolen et al. 2003). Fish in control groups were maintained in the transparent

compartment for an equivalent duration (10 min) but saw no public demonstration.

The experimental conditions varied according to the patterns of food delivery to the 2 shoals during the public demonstration, with demonstrators feeding on either a “2|6” or a “4|8” schedule (i.e., receiving either 2 and 6 or 4 and 8 food deliveries per 10 min session at the public-poor [personal-rich] and public-rich [personal-poor] feeders, respectively). Fish that were exposed to, for example, a 6|2 training schedule followed by a 4|8 demonstration are hereafter referred to as “6|2 then 4|8.”

Preference test after public demonstration

Finally, fish were given a further choice test to determine their choice of feeder (public rich or public poor). After the public demonstration, the demonstrators and any remaining food were removed from the experimental tank. The observer was then released from the central compartment and its location recorded every 6 s for the following 90 s. No food was provided during the preference test. Accordingly, choice of a feeder is potentially indicative of reliance on either personal or public information. Our analysis focuses on the behavior of the fish during this choice test.

Data analysis

In total, preference data were collected from 120 fish, spread evenly across the 6 conditions. 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 feeder preference as the difference (public rich minus public poor) in the number of instances that the fish was present in each goal zone during the preference test. Linear mixed-effects models (LMMs) (Pinheiro and Bates 2000) were fitted to the data and orthogonal repeated contrasts used to test for predicted differences between pairs of treatment groups using 1) a vector of contrasts grouped by personal information feeding regime and ordered by public information feeding regime and 2) a contrast vector grouped by public information feeding regime. Training batch was included as a random effect in the model. This results in uneven degrees of freedom (df) between contrasts because some fish from certain batches were subsequently assigned to 1 treatment group (fixed effect) and the remaining fish to another treatment group, where treatment groups shared a common training regime (Pinheiro and Bates 2000).

RESULTS

We found that fish in the control groups, that received no public demonstration, showed a significant preference for the personal-rich feeder (one-sample *t*-test against a test mean of 0: control 1 (6|2): $t = 4.87$, $n = 20$, $P < 0.001$ and control 2 (8|4): $t = 2.24$, $n = 20$, $P = 0.037$; Figure 2), confirming that personal training was effective. There was no significant difference between feeder preference for fish in the 6|2 and 8|4 controls (contrast from a LMM: $t = 0.98$, $df = 92$, $P = 0.330$).

Fish in the 2 treatment groups that received a 2|6 feeding regime during the public demonstration spent significantly more time near the public-rich (personal-poor) feeder than those in the control groups (contrasts comparing “6|2 then 2|6” against 6|2 control: $t = 4.31$, $df = 21$, $P < 0.001$ and “8|4 then 2|6” against 8|4 control: $t = 2.56$, $df = 93$, $P = 0.012$; Figure 2), and fish exposed to a 4|8 public feeding regime copied at a significantly elevated rate to those exposed to a 2|6 regime (contrasts comparing “6|2 then 4|8” against “6|2 then 2|6”: $t = 3.47$, $df = 21$, $P = 0.002$ and “8|4 then 4|8” against “8|4 then 2|6”: $t = 2.54$, $df = 93$, $P = 0.013$; Figure 2).

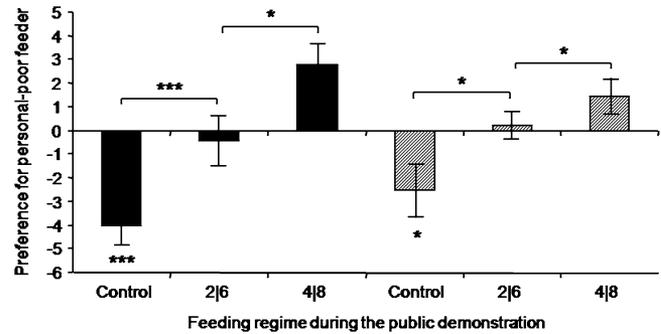


Figure 2

Mean \pm standard error difference (personal poor minus personal rich) in the number of instances that the fish was present in the “goal zone” around each feeder (from instantaneous sampling of the fish’s location every 6 s for the first 90 s following the start of the choice test), in fish trained on a 6|2 (i.e., 6 and 2 deliveries to rich and poor feeders, respectively; black bars) or 8|4 (hashed bars) regime and subsequently exposed to either a 2|6 or a 4|8 public demonstration (denoted as “2|6” or “4|8,” respectively). Controls received no public demonstration (see text for full details). Asterisks denote either a significant difference from zero (in controls) or a significant difference between groups: *** $P < 0.001$, * $P < 0.05$.

In contrast, despite a weak tendency for fish exposed to the 6|2 personal training regime to copy more than those receiving the 8|4 regime (Figure 2), there was no evidence that the time spent at the public-rich feeder was significantly affected by the earlier rate of feeding at the alternative feeder: the 2 groups that received a 2|6 feeding regime during the public demonstration copied at an equal rate (contrast comparing “8|4 then 2|6” against “6|2 then 2|6”: $t = 0.44$, $df = 92$, $P = 0.662$) as did the 2 groups exposed to a 4|8 public feeding regime (contrast comparing “8|4 then 4|8” against “6|2 then 4|8”: $t = 0.68$, $df = 22$, $P = 0.501$), irrespective of their personal information. These results show that the probability of a subject choosing the public-rich feeder increased with the payoff to the demonstrators, but this choice was unaffected by the payoffs subjects themselves received during personal training.

DISCUSSION

The results of this experiment provide a clear indication of the social learning strategy being deployed by nine-spined sticklebacks. The probability that observer fish switch from reliance on personal to social sources of information (i.e., the extent to which they copy) was found to be dependent solely on the observed returns to demonstrators, with copying increasing with the absolute rate of feeding by demonstrators at the rich feeder. This is exactly the behavior predicted by the “proportional observation” rule (Schlag 1998; Laland 2004) and provides compelling evidence that these fish are able to use an algorithm, theoretically demonstrated to be optimally efficient, to guide their foraging behavior. There was a weak, but nonsignificant, tendency for fish that had received lower returns in personal training to copy more than those that had received higher returns, but this is not sufficient to support interpretation in terms of utilization of a “proportional reservation” or “proportional imitation” rule. Nor is the pattern of results well explained by other social learning strategies: conformist bias, prestige bias, and size/rank/age-biased copying models would all predict different patterns (Boyd and Richerson 1985; Henrich and McElreath 2003; Laland 2004).

The fact that, under test, the sticklebacks’ responses to public information were unaffected by their personal training regime implies that in this species, an individual’s prior rate of foraging success does not affect the likelihood of adopting the

behavior of other fish. However, it does not follow from this that the individual's personal experience as a whole is irrelevant, as our previous experiments have established that if nine-spined sticklebacks have no prior knowledge of the feeders, they will copy at a higher rate (Coolen et al. 2003). Thus, although the rate of copying here appears solely dependent on the payoff to the demonstrator, previous studies have established that the decision to copy also is affected by both personal and public information. It could be that using a greater food delivery rate during training (e.g., 10/6) might uncover an effect of the rate of feeding during personal training on the fish's propensity to copy, in line with the existing trends in the data. However, it should be noted that using a lower rate during the public demonstration (0/4) appears to have little effect on the rate of copying in fish on the 6/2 training regime (Kendal et al. 2009).

Our results also provide insights into the information that nine-spined sticklebacks are utilizing when making socially mediated foraging decisions. The increase in their propensity to copy appears to increase with the absolute amount of food provided by the rich feeder rather than the relative proportion of food provided by each (i.e., they showed elevated levels of copying when the rich feeder dispensed 8 feeds per session compared with 6 feeds per session, even though the relative proportion of food provided by the rich feeder was lower: 0.67 compared with 0.75). This raises the possibility that nine-spined sticklebacks may be able to count and remember the absolute quantity of food delivered to each feeder (arguably a cognitively more challenging task than estimating the number of shoaling conspecifics) and, unlike some other species of fish, do not appear to make assessments based on proportions, at least within the range of values used here (Agrillo et al. 2008).

It is no trivial matter for an animal to evaluate the relative quality of 2 resources, such as the profitabilities of 2 food patches, through observation alone and without directly sampling the resources. Indeed, several recent studies in mammals, birds, and fish fail to find evidence of public information use (Giraldeau et al. 2002; Coolen et al. 2003; Valone 2007), so it cannot be construed as given. Although many vertebrates have been shown differentially to approach sites with high conspecific activity at the time of demonstration, it is much more challenging for animals to evaluate the profitability of alternative food sites through observation alone and to select the richer of the 2 sites at a later time. For instance, three-spined sticklebacks, a close relative of nine-spined sticklebacks, will consistently join conspecifics feeding at rich food patch in preference to otherwise similar shoals at a poor patch (Webster and Hart 2006) but fail the more challenging public information use test, where information about patch quality must be gained through observational learning and retained to guide subsequent patch choices (Coolen et al. 2003). In contrast, nine-spined sticklebacks are clearly capable of gauging the relative profitability of food patches through observing the feeding activity of others without directly sampling patch quality themselves (this study; Coolen et al. 2003, 2005), that is, to engage in public information use. Despite extensive experimental investigation by our laboratory, incorporating both asocial and social learning tasks, we have yet to find any differences in the learning performance of three-spined and nine-spined sticklebacks, other than in their propensity to utilize social information. The present study builds on these findings to confirm an unusually proficient use of social learning in this species. The observation of a highly proficient, yet specific, form of learning in a freshwater fish, which is absent in a close relative, is evocative of established adaptive specializations in animal learning, such as the enhanced memory capacity of food-storing birds (Krebs et al. 1989; Healy and Krebs 1992;

Clayton and Krebs 1994) or the preferential acquisition of conspecific song by passerine birds (Marler and Tamura 1964). Our findings therefore support the view that the taxonomic distribution of cognitive capabilities may be better explained by convergent evolution, driven by specific agents of selection, than by how closely a species is related to humans (Shettleworth 2001; Pepperberg 2002; Emery and Clayton 2004; Holekamp et al. 2007).

Theoretical findings suggest that social foraging and information pooling may enhance the efficiency with which group-living animals harvest complex multicomponent diets in a cumulative manner (van der Post and Hogeweg 2008). Such theory raises the possibility that the dietary traditions observed in many animals, including fish, birds, rodents, cetaceans, and primates such as chimpanzees (Warner 1988; Whiten et al. 1999; Rendell and Whitehead 2001; Fragaszy and Perry 2003; van Schaik et al. 2003), may be the result of several generations of cumulative knowledge gain. However, such claims have encountered scepticism because it has not been clear that animals possess the social learning mechanisms capable of supporting cumulative acquisition of knowledge (Galef 1992; Tomasello 1994). Theoretical work by Schlag (1998, 1999) established that the use of a relatively simple rule by individuals (proportional copying) could lead to a surprisingly complex outcome in a population (cumulative knowledge gain). In this respect, our results may be of general significance because they establish that the proportional observation rule, which possesses the hill-climbing properties necessary to allow optimal solutions to be reached over repeated iterations, is actually observed in nature. The deployment of a strategy with this potential ratcheting quality has, to our knowledge, never been demonstrated before in a nonhuman and has hitherto been considered absent in animals. Utilization of such a strategy by nine-spined sticklebacks may allow them to exhibit cumulative increases in the efficiency with which they exploit diverse prey in their natural environments, for instance, as they colonize new regions. More generally, it may be worth investigating to what extent traditional behavior in other species is reliant on the proportional observational rule because this would reflect on the species' capability for cumulative culture. Further work is needed to shed light on this exciting possibility.

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