

Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues

Isabelle Coolen,^a Ashley J.W. Ward,^b Paul J.B. Hart,^b and Kevin N. Laland^a

^aSub-Department of Animal Behaviour, Cambridge University, Madingley, Cambridge CB3 8AA, UK, and ^bDepartment of Biology, University of Leicester, LE1 7RH, UK

Social animals can observe others' behavior and in the process acquire information of varying quality about a given resource. Theoretical models predict that blind copying of others' behavior is more likely when individuals are only able to observe the decisions (here "social cues") of others rather than the cues (here "public information") on which such decisions are based. We investigated information use by nine-spined sticklebacks (*Pungitius pungitius*) in a two-patch foraging context. Social cues were provided by the number of demonstrator fish present at each patch (two versus six), which either conflicted with the demonstrators' observed feeding rate at each patch (public information) or was the only information available. Consistent with predictions, observers preferred the patch previously associated with six demonstrators when social cues were the only available source of information but preferred the patch previously associated with two demonstrators ("rich" patch) when also provided with public information. On the bases of these experiments, we argue that it is because these fish preferentially base decisions on public information rather than social cues that they can potentially avoid engaging in erroneous informational cascades. Thus, the availability of public information can help social animals make adaptive decisions. *Key words:* copying, foraging, informational cascades, nine-spined sticklebacks, public information, social cues. [*Behav Ecol*]

Social animals have the opportunity to observe others and to learn from them how and where to feed (Galef and Giraldeau, 2001), as well as to acquire other information, such as with whom to mate (Nordell and Valone, 1998) or fight (McGregor et al., 2001). When it comes to assessing patch quality, group foragers can also potentially pick up on information transmitted inadvertently by others through their behavior and decisions. Inadvertent social information can be divided into "social cues," where information about a resource is derived from others' decisions, and "public information," where it is derived from the direct observation of others exploiting the resource (Danchin et al., 2004). Dall et al. (2005) further stipulate that social cues provide discrete information about the location, presence, or absence of features, whereas public information provides graded information about the quality of features. Public information has been shown to be used by some species (nine-spined sticklebacks *Pungitius pungitius*, Coolen et al., 2003; van Bergen et al., 2004; red crossbills *Loxia curvirostra*, Smith et al., 1999; Starlings *Sturnus vulgaris*, Templeton and Giraldeau, 1995, 1996) but not others (three-spined sticklebacks *Gasterosteus aculeatus*, Coolen et al., 2003; blackbirds *Turdus merula*, Smith et al., 2001; Budgerigars *Melopsittacus undulatus*, Valone and Giraldeau, 1993). Conceivably, public information may not always be easy to acquire, and consequently simpler social cues may sometimes be used instead.

In natural circumstances, the presence of a forager at a patch is interpreted as a manifestation of its adaptive decision making. Hence, observer conspecifics could make in-

ferences about a patch's profitability based on the number of foragers that seemingly have chosen it. In addition to conformity to ideal free distribution (Fretwell and Lucas, 1970), there are many examples of animal populations in which individuals use the number of conspecifics in a group to decide whether or not to join. For instance, Gotceitas and Colgan (1991) found that three-spined sticklebacks prefer to stay near a large rather than a small group of feeding conspecifics, independent of their feeding rate, suggesting foraging or antipredator benefits (but see Krause, 1992). Similarly, Pomiankowski (1990) reports that the rate at which females enter a given male's territory is correlated to the number of females already present on his territory. However, while alleviating individuals from themselves incurring the cost of sampling, social learning could, at least in theory, also potentially transmit suboptimal foraging information, leading to short-term maladaptive traditions (Day et al., 2001; Giraldeau et al., 2002; Laland and Williams, 1998; Pongrácz et al., 2003) or mate preferences (Witte and Massmann, 2003; Witte and Nolte, 2002). The quality of decisions depends on the reliability of the information used, which will in part depend on whether it is graded (public information) or discrete (social cues; Dall et al., 2005).

Although the trade-off between personal and social information has been extensively investigated, both theoretically and empirically (see Kendal et al., in press), the trade-off between two types of social information has been much less studied. A recent framework originating in economics however considers a scenario where it would be optimal for individuals to copy others' choices without regard to their personal information, thereby leading to informational cascades (Bikhchandani et al., 1992, 1998; Giraldeau et al., 2002). Although not meant precisely to study the trade-off between social cues and public information use, the informational cascade framework makes precise predictions relevant to that trade-off. Indeed, irrespective of whether blind copying of others' behavior results in the spread of accurate or inaccurate information, theoretical analyses predict that copying the majority is more likely when individuals are only able

Address correspondence to I. Coolen, who is now at the Institut de Recherche en Biologie de l'Insecte, UMR CNRS 6035, Université de Tours, 37200 Tours, France. E-mail: icoolen@yakcommunication.com. K.N. Laland is now at the Centre for Social Learning and Cognitive Evolution, School of Biology, University of St. Andrews, Bute Medical Building, Queen's Terrace, St. Andrews, Fife, Scotland KY16 9TS, UK.

Received 8 December 2004; revised 5 May 2005; accepted 9 May 2005.

to observe the decisions of others (social cues) rather than when they also have access to the cues (public information) on which those decisions are based. Here, we test this prediction by exploring the patch choices of nine-spined sticklebacks provided with social cues only (i.e., number of demonstrators present at each patch) or with both social cues and public information (i.e., demonstrators' feeding rate). Although we do not claim that information cascades are necessarily or even more commonly erroneous, discriminating between the use of public information and social cues requires that the information conveyed by one conflicts with the other, a situation reminiscent of an erroneous informational cascade.

Nine-spined sticklebacks are an appropriate species for this investigation because they are known to distribute according to the ideal free distribution (van Bergen, 2004), which means that the numbers of individuals at patches potentially provides relevant social cues about its quality. Moreover, nine-spined sticklebacks are known to be capable of using the relative feeding rates of demonstrators' to determine the richer of two patches (Coolen et al., 2003; van Bergen et al., 2004) and thus to be able to exploit public information concerning patch quality.

In the first experiment, we provided hungry naive observers solely with social cues concerning the patch, in the form of the number of conspecifics present in the vicinity of each of two patches, and then allowed them to choose a patch after the demonstrators had been removed. We predicted that observer fish would rely on those prior social cues because no public information was available and thus prefer the patch previously associated with the greatest number of conspecifics. In the second experiment, naive observers were provided with public information that conflicted with the concomitant social cues available. Observers were then given a choice between a patch that was previously associated with many conspecifics feeding at a low rate and an alternative patch associated with few conspecifics feeding at a high rate. We expected observers to use the public information available to them and thus prefer the "rich" patch. In order to ensure that patch choice in Experiment 2 followed from prior observation of feeding rates, a control experiment was performed to assess whether observers could choose a patch based on chemical cues from bloodworms alone.

METHODS

Subjects

We used a total of 120 nine-spined sticklebacks (mean \pm SD body length: 36.18 ± 2.73 mm) of undetermined sex in this study. Eight fish served as demonstrators in both experiments, but the composition of the demonstrator shoals was varied from one trial to the next to prevent pseudoreplication. Demonstrator shoals were drawn at random from a pool of 40 fish for each experiment/replicate. These fish were chosen to be of similar size and competitive ability, so as to match the assumptions of the ideal free distribution, that is, relative patch quality is adequately indicated by the number of foragers in each patch. Twenty naive fish served as observers in each experiment. All fish were collected at Melton Brook, Leicester, U.K. ($52^{\circ} 36' N$, $1^{\circ} 7' W$). They were kept in tanks at a water temperature of $11^{\circ}C$ and fed on frozen bloodworms. Testing occurred in summer 2004. In order to prevent the fish coming into breeding condition, no vegetation was provided in the holding or experimental tanks, an element reported to be partially responsible for the triggering of reproductive behavior (Keenleyside, 1955; Tinbergen, 1951), and the fish were kept on a stable light:dark cycle. Moreover, the food deprivation

undergone by fish before testing (36 h) almost certainly generated a motivation to feed sufficient to inhibit any reproductive behavior at test (Keenleyside, 1955), while increasing the likelihood that observers' decisions at test would be food patch choices.

Apparatus

The experimental tank (90×30 cm long and filled to a depth of 20 cm) was divided into three sections of equal sizes (see Figure 1). One feeder was placed in each end section of the tank. The feeders were 25-cm-high columns with opaque sides facing the observer but transparent front facing the demonstrators, who would peck at the bloodworms as they sank to the bottom of the column, where they were eaten through a slot. This design prolonged the demonstration, making it a salient cue for the observer. The patches were defined as the zones immediately surrounding the feeders from the experimenter's view and delineated by visual aids available to the experimenter. Prior to introducing the fish, partitions were installed as shown in Figure 1. Opaque partitions (sheets of white Perspex) were also placed along the patch delimitations to prevent the demonstrators from interacting with feeders before the start of the experiment. A transparent plastic bottle was opened up so as to form a semicircular compartment of 19.5 cm diameter and 25 cm height. It was placed along the wall in the central section and served as the observer compartment (see Figure 1).

Procedure

Prior to experiments, observer fish were familiarized with the feeders used in the experiments and received their daily meals through them six times to promote the association of the feeders with food. This training occurred in the holding tank, where only one feeder was introduced, in order to prevent biasing toward specific areas in the experimental tank or toward one of the two feeders prior to demonstration. Although we have not tested whether 6 days of exposure to feeders sufficed to associate them with food, we did observe that the number of fish attending the feeders increased as the feeding session advanced, and by the sixth day of exposure, all fish

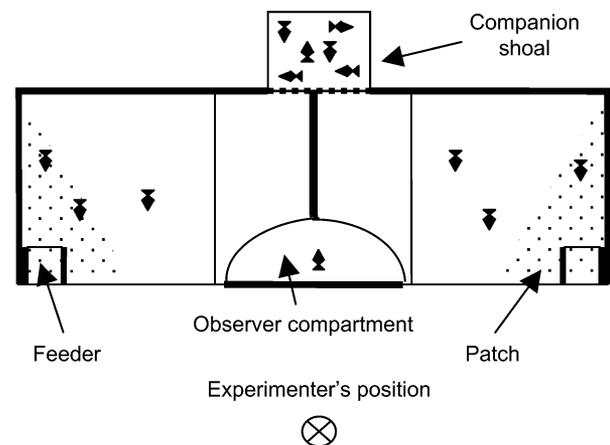


Figure 1

Plan view of the experimental tank set up during the observation period. Thick lines represent opaque partitions, thin lines represent transparent partitions, and dots represent patches (i.e., zones immediately surrounding the feeders). The hatched line between the central section of the experimental tank and the tank holding the companion shoal indicates a one-way mirror allowing the observer to see the companion shoal but not the reverse.

had been seen attending to the feeders and obtaining food through them. Previous studies carried in our laboratory have established that this is more than enough time for fish to associate the feeder with food. Also, demonstrator fish were placed in the empty experimental tank (without partitions or feeders) for at least 12 h on the day preceding their testing in order to reduce any exploratory behavior during testing (Mikheev and Andreev, 1993). At all times, and for all experiments, a companion shoal of 6 fish drawn at random from a pool of 20 fish was placed in an adjacent tank (see Figure 1). The size of the companion shoal was set at six so that the “six-demonstrator” feeder could not appear safer than the central section. The adjacent tank measured 15 cm long by 12 cm wide by 20 cm deep. Importantly, the front panel of the adjacent tank that faced the experimental aquarium was made of one-way glass. As a consequence, although the observer fish could see the companion shoal, the latter could neither see the observer nor provide cues for the focal fish about which feeder to visit.

For both Experiments 1 and 2, two groups of demonstrators, one consisting of 2 fish the other one of 6 fish, chosen at random among the set of 40 similar-sized demonstrators were placed in the end sections of the tank. Patch status was randomly assigned in a balanced way so that the patch associated with six demonstrators was presented 10 times on the left-hand side and 10 times on the right-hand side of the tank. An observer was then placed in the observer compartment. After all fish had settled for 10 min, the opaque partitions hiding the feeders were removed and the observation period started.

The observation period lasted for 10 min. In Experiment 1, where only social cues were available, there was no food provided in any of the patches. This way, we investigated whether nine-spined sticklebacks relied on social cues (i.e., number of demonstrators present) when no other information was available. In Experiment 2, where both social cues and public information were available, demonstrators were observed eating. The group of two demonstrators fed at a “rich” patch that delivered food (two–three bloodworms in water) at 1 min 30 s and every 1 min 30 s after that (i.e., six times during the 10-min observation period). The group of six demonstrators fed at a “poor” patch that delivered two–three bloodworms at 1 min 30 s and 6 min (i.e., twice during the observation period). Although unable to see the food delivery directly, observers could witness the feeding behavior of the demonstrators and thus the success of demonstrator groups on both patches.

After the observation period, the observer was visually isolated from the rest of the tank by opaque partitions placed around the central section, and the demonstrators as well as any remaining bloodworms were removed. The removal of the demonstrators controls for any antipredator benefits that could be gained by associating with the larger demonstrator group. The plastic bottle was then removed allowing the observer to swim freely in the central section for about 5 min. This delay was introduced to ensure that the subsequent patch choice of the subject was not influenced by shoaling preferences and was solely reliant on its memory of inferred patch quality. A black fabric hide was pulled in front of the tank, concealing the experimenter and laboratory surroundings to the observer fish in order to avoid any biasing of the observer’s decision by cues other than prior demonstration. All remaining partitions in the tank were then removed remotely and the testing period started. The subject’s position in the tank was recorded, together with other relevant data, as detailed below. The test continued until 1 min 30 s had elapsed, and if the observer did not reach a patch (Figure 1) during that time, the test continued until it did.

It is unlikely that, at test, the prior location of the rich food patch was indicated to the observer fish by residual olfactory cues, first because sticklebacks predominantly hunt by sight and have been reported to have a relatively poor sense of smell (Honkanen and Ekstrom, 1992), second because water with a bloodworm flavor was delivered on the poor side whenever food was delivered on the rich side, and third because the removal of the demonstrators and partitions prior to test generated disturbance of the tank water. However, to test for this possibility, we first performed a control experiment in which bloodworm juice was delivered six times during the 10-min observation period on one side (“bloodworm”) while the other side (“no cues”) received plain water. In the event that the absence of demonstrators in the control experiment reduced water disturbance, this would have resulted in higher concentrations of bloodworm cues in and around the feeder delivering such cues, thereby enhancing the difference between feeders and thus rendering our test conservative.

Behavioral data and statistical analysis

Data collection and statistical analyses were similar for all experiments. During the testing period, the position of the fish was scan sampled every 10 s for a minute and a half. We defined a fish as in a zone (section or patch) when its head, up to the pectoral fins, was in that zone. We focused our analysis on the subject’s use of the patches because the choice on the part of the fish as to which side it preferred is clearer when in either patch than when in the remaining part of the end sections. For each experiment, using chi-square tests, we compared the proportion of observers that entered first the patch that had previously been associated with the large group of demonstrators to the proportion expected from a 50:50 distribution. We also compared with an analysis of variance, the proportion of scans in which a fish was seen in each section. Where the data were not normal and could not be normalized, we analyzed ranked data (Potvin and Roff, 1993).

RESULTS

Control experiment: solely chemical cues available

The patch decision of observers did not appear to be driven by bloodworm chemical cues. Among the 20 fish tested, 9 fish visited first the patch that previously delivered bloodworm cues, whereas 11 fish visited first the alternate patch delivering plain water ($\chi^2_1 = 0.2$, $p = .65$). Moreover, observers preferentially stayed in the central section, near the companion shoal, than near any feeder ($F_{2,57} = 55.89$, $p < .001$; Figure 2). Those results rule out the possibility that chemical cues play a significant role in the observers’ patch choice. They also indicate that the companion shoal placed near the central section made that section attractive to subjects, most likely through risk dilution.

Experiment 1: only social cues available

Observers relied on social cues when this was the only information they could access concerning patch quality. Among the 20 fish tested, 16 chose to visit first the patch associated with the larger number of demonstrators a few minutes earlier ($\chi^2_1 = 7.2$, $p = .007$) and did so despite the absence of the demonstrators at the moment of choice. Moreover, observers spent on average more time in the central section and at the patch that was previously associated with the greater number of demonstrators than at the alternative patch ($F_{2,57} = 27.45$, $p < .001$; Figure 3).

Also, when compared to the control experiment, observers in Experiment 1 spent more time in the patch that previously

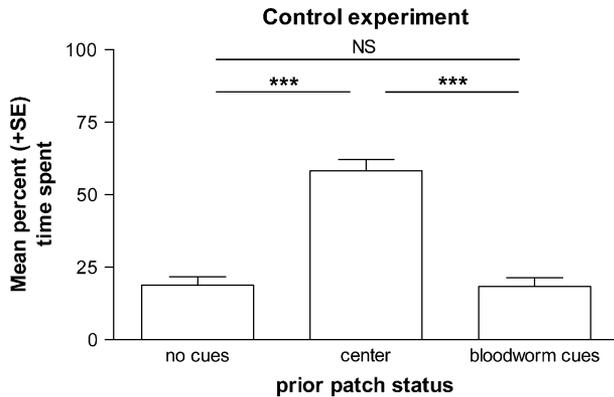


Figure 2 Mean percent (+SE) time observers spent in each patch ($n = 20$) after chemical cues were released on the bloodworm side only during the observation period. Statistics showed refer to post hoc Tukey tests' pairwise comparisons among sections. *** $p < .001$.

contained six demonstrators (independent sample t test: $t_{38} = -3.83$, $p < .001$) and less time in the patch that previously contained two demonstrators ($t_{38} = 2.22$, $p = .032$) or in the center ($t_{30.4} = 2.68$, $p = .012$; Figures 1 and 2). However, after controlling for the familywise error rate, the decrease in time spent in the patch previously associated with two demonstrators was marginally nonsignificant ($\alpha' = 0.017$).

Experiment 2: both social cues and public information available

When observers received both social cues and public information, they behaved as if they favored public information in their assessment of relative patch quality. Only 4 of the 20 observers tested chose to visit first the patch used by the 6 demonstrators, this patch also being the poor patch, with the other 16 choosing the rich patch where only 2 demonstrators had been seen feeding ($\chi^2_1 = 7.2$, $p = .007$). Moreover, the observers spent predominantly more time in the patch used previously by two demonstrators (rich patch) than in either the patch used by six (poor patch) or the central section, ($F_{2,57} = 28.73$, $p < .001$; Figure 4). The fact that the control experiment failed to show an effect of chemical cues on patch visit implies that observers' decisions were based alternatively on prior demonstration. The results thus suggest that

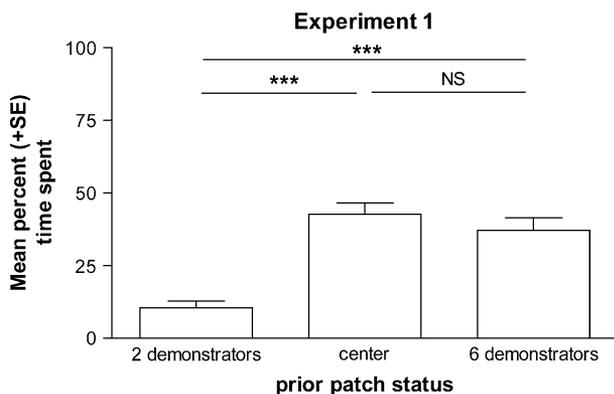


Figure 3 Mean percent (+SE) time observers spent in each patch ($n = 20$) after they collected indirect information about relative patch quality during the observation period. Statistics showed refer to post hoc Tukey tests' pairwise comparisons among sections. *** $p < .001$.

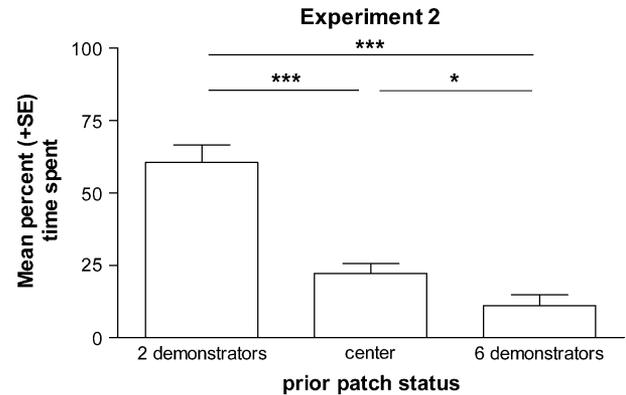


Figure 4 Mean percent (+SE) time observers spent in each patch ($n = 20$) after they collected both direct and indirect information about relative patch quality during the observation period. Statistics showed refer to post hoc Tukey tests' pairwise comparisons among sections. * $p < .05$, *** $p < .001$.

nine-spined sticklebacks preferentially used the information they derived themselves from observing the success of demonstrators (public information) rather than from just their number (social cues).

Also, when compared to the control experiment, observers in Experiment 2 spent more time in the patch that previously contained two demonstrators (independent sample t test: $t_{38} = -6.70$, $p < .001$), spent less time in the center ($t_{31.2} = 6.99$, $p < .001$), and did not change the time they spent in the patch that previously contained six demonstrators ($t_{38} = 0.77$, $p = .448$). Results were unchanged after we controlled for familywise error rate ($\alpha' = 0.017$).

DISCUSSION

Consistent with our predictions, our experiments provide evidence that nine-spined sticklebacks choose food patches using social cues when it is the only available information source but preferentially rely on public information when it is also available.

In Experiment 1, nine-spined sticklebacks seemingly attributed a higher intrinsic value to the patch visited earlier by six individuals compared with an alternative patch visited by two individuals. We argue that antipredatory motivations could not have led the subjects to swim to the side previously containing the larger group; no demonstrator fish was present at either patch at the moment of choice, and the continued presence of a companion shoal near the central section made this latter section the safest one (see Control Experiment: Solely Chemical Cues Available). As a consequence, any visit out of the central section, and even more so to any patch, was made at the expense of time spent near the companion shoal. Also, fish had been trained to associate the feeders with food, and this may have rendered the presence of demonstrators an informative cue about patch quality even in the absence of food (Giraldeau et al., 2002). The combination of these facts suggests that the preference detected related to the subjects' assessments of relative patch quality rather than to putative risk-dilution benefits. Whatever the exact nature of the information conveyed by the former presence of the two groups of demonstrators, nine-spined stickleback observers copied the majority in their patch choice when they could witness the decisions made by others (social cues).

However, in Experiment 2, when observers also had access to public information through observation of the feeding

rate, they preferred to rely on public information to make their patch choice. Nine-spined sticklebacks have recently been shown to prefer the richer of two patches when observing two groups of conspecifics of equal sizes feeding at different rates (public information; Coolen et al., 2003). Not only did the fish in the present study also prefer the rich patch according to public information (Experiment 2), they did so despite strong conflicting social cues, information that was taken into account when it was the only available source (Experiment 1). Our results thus imply that nine-spined sticklebacks weight public information more heavily than social cues. This is consistent with Templeton's findings on starlings that animals may pay more attention to direct cues about the resource than to the decisions made by others (Templeton, 1998; Templeton and Giraldeau, 1995, 1996).

At first sight, our interpretation may appear to contradict the recent findings of Hoare et al. (2004) that hungry banded killifish (*Fundulus diaphanous*) prefer to form large groups when expecting a predator but small groups when expecting food. Although groups can generate competition or provide protection, those outcomes require that groups are present. Once gone, those properties of groups are no longer valid. Not only were group members still present in the study of Hoare et al. (2004), but subjects also received food or predation cues during the testing period, thereby eliciting a concomitant foraging or antipredatory behavior and allowing for an interpretation in terms of competition or risk dilution. In our study, however, no such cues were given at test; chemical cues in the concentrations we used have been shown not to affect patch visit decisions (control experiment), and the presence of a companion shoal near the central section made it a safer place than any patch. Moreover, the absence of demonstrators at the moment of choice made any competition or dilution risk from those demonstrator groups outdated. For these reasons, we maintain that our results relate instead to the information conveyed by the demonstrators about patch quality.

Under an ideal free distribution, the number of fish that have chosen each patch could provide reliable social cues about relative patch quality. It should be noted that the nature of patches will have an impact on the extent to which this is true. Indeed, when prey availability is static, the patches vary in amounts and the resource is exhaustible and nonrenewable. Therefore, the more foragers exploit a patch, the faster will this patch deplete. In these conditions, two fish feeding at a patch may be perceived as depleting that patch less than would six fish, which could, in principle, account for the pattern of results observed in Experiment 2. Conversely, when the resource is renewable and the patches vary in the rate at which they replenish, the number of foragers at a patch may affect the access to the resource but will have no impact on patch richness. The number of foragers seen at a patch should thus not convey information signifying depletion. It is this latter situation that best represents our experimental subjects and procedure. Stream-dwelling fish like nine-spined sticklebacks commonly feed on drifting prey, thereby naturally experiencing continuous input patches. Although nine-spined sticklebacks may be able to distribute ideally and freely when exploiting static prey and may occasionally encounter the case in the field, in our experiments they have been trained specifically on a continuous input schedule. The demonstrator's behavior is also in response to a renewable resource supply. Finally, the topology of a stream will create spatial heterogeneity in terms of both water flow characteristics and suitable feeding locations, thus creating areas that are better for drift food than are others. The regularities of the streambed over the medium term are likely to produce a strong temporal autocorrelation between food availability and location. For these reasons, we judge it unlikely that the two-fish

demonstrator shoals were perceived by the subjects as having depleted their patch less than the six-fish shoal. Furthermore, had our subjects been drawing inferences about patch richness on the basis of number of past patch exploiters, we would not expect the pattern of results reported in Experiment 1. The most plausible explanation for our findings is that the elevated rate at which the two-fish shoal fed relative to the six-fish shoal (public information) led the observers to value the former patch more than the alternative.

Although our study is relevant to all circumstances under which animals make decisions based on social cues, it has particular implications for the outcome of informational cascades. Informational cascades, defined as blind copying of the behavior of others, are predicted to occur when observers make decisions on the basis of social cues but are thought to be less likely when they also have access to the cues on which the others based their decisions (public information; Bikhchandani et al., 1992, 1998; Giraldeau et al., 2002). One might argue that in Experiment 1, fish could not engage in an erroneous cascade per se; none of the feeders delivered any food, and thus adopting the behavior of others apparently had no negative consequences on fitness. However, when fish chose the patch previously containing the larger shoal, they did so at the expense of being near the companion shoal, and thus any copying of the decisions of others was here traded against actual risk dilution. In any case, observers did behave consistently with an informational cascade by following the patch choice of the majority. Our results thus support the prediction that the lack of any public information or resource cues about patch quality may set the conditions for an informational cascade to start. Moreover, the results of Experiment 2 support the prediction that access to public information and a preference for public information over social cues could help to prevent an erroneous informational cascade from occurring.

Given that informational cascades may be associated with fitness costs, they may conceivably be one source of selection favoring the evolution of the capacity for the use of public information. The collection of public information may thus provide the direct information necessary to avoid erroneous informational cascades, and animal species that can and do collect public information may have a selective advantage over those that do not (Coolen et al., 2003). Therefore, public information not only provides additional information to that gathered by direct sampling (Valone and Templeton, 2002), but its use can also help individuals to avoid the erroneous and costly copying of others' decisions.

It should be noted, however, that although informational cascades are most intriguing when they lead to erroneous copying, we anticipate that they equally, and probably more frequently, lead to correct copying. Giraldeau et al. (2002) suggest that informational cascades could be behind collective phenomena such as night roost site selection, false-alarm collective flights, or mate-choice copying. In mate-choice situations, copying the mate choices of others may conceivably lead to maladaptive decisions. Indeed, female sailfin mollies (*Poecilia latipinna*) can forego their natural preference for large males to copy other females' mate choice (Witte and Massmann, 2003; Witte and Noltemeier, 2002) and maintain this preference for several weeks. However, one cannot ignore the cases where blind copying of others' mate choice allows females to identify a good mate from older and more experienced females (Nordell and Valone, 1998). Regarding alarm flight, only a few fish need to be informed to change the direction of the whole school (Couzin et al., 2005), with the remaining engaging in an informational cascade by blindly following the decisions of others. The effect though is beneficial as the school would turn away from or swim round the

predator and escape an attack. But even when danger is not impending, false-alarm flights (i.e., erroneous cascade) may be the optimal solution; the benefit of avoiding predation often largely exceeds the cost of losing feeding time. Moreover, those costs can be further reduced by giving more weight to multiple departures, which are more likely to be predator driven, than to single departures (Lima, 1994, 1995).

The informational cascade framework originated in economics (Bikhchandani et al., 1992, 1998), and the majority of studies on this topic have been devoted to humans (Anderson and Holt, 1996, 1997; Hung and Plott, 2001). Our study suggests that informational cascades can also be studied empirically, using animals. Moreover, several empirical studies on non-human animals could be reinterpreted in terms of informational cascades (Bates and Chappell, 2002; Laland and Williams, 1998; Pomiankowski, 1990; Schlupp et al., 1994; Witte and Nolte, 2002). There are grounds for suspecting that informational cascades are of relevance to a wide range of topics in behavioral ecology, including foraging, mate choice, information centers, social learning, and ideal free distributions, and we endorse the suggestion of Giraldeau et al. (2002) that this perspective warrants more attention.

J. Kendal, S. Reader, M. Rekers, H. Snippe, T. Valone, Y. van Bergen, and two anonymous reviewers provided helpful comments on a previous version of the manuscript. I.C. was funded by a Fyssen Foundation Postdoctoral Fellowship and a European Community, Information Society Technologies (IST) Programme, Future and Emergent Technologies (FET), Lifelike Perception Systems action postdoctoral fellowship, A.J.W.W. is a postdoctoral associate funded by a Natural Environment Research Council grant to P.J.B.H., and K.N.L. was funded by a Royal Society University Research Fellowship.

REFERENCES

- Anderson L, Holt C, 1996. Classroom games: informational cascades. *J Econ Perspect* 10:187–193.
- Anderson L, Holt C, 1997. Information cascades in the laboratory. *Am Econ Rev* 87:847–862.
- Bates L, Chappell J, 2002. Inhibition of optimal behavior by social transmission in the guppy depends on shoaling. *Behav Ecol* 13:827–831.
- Bikhchandani S, Hirshleifer D, Welch I, 1992. A theory of fads, fashion, custom, and cultural changes as informational cascades. *J Polit Econ* 100:992–1026.
- Bikhchandani S, Hirshleifer D, Welch I, 1998. Learning from the behavior of others: conformity fads and informational cascades. *J Econ Perspect* 12:151–170.
- Coolen I, van Bergen Y, Day RL, Laland KN, 2003. Species difference in adaptive use of public information by sticklebacks. *Proc R Soc Lond B* 270:2413–2419.
- Couzin ID, Krause J, Franks NR, Levin SA, 2005. Effective leadership and decision-making in animal groups on the move. *Nature* 433:513–516.
- Dall SRX, Giraldeau L-A, 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 L-A, Valone TJ, Wagner RH, 2004. Public information: from nosy neighbors to cultural evolution. *Science* 305:487–491.
- Day RL, MacDonald T, Brown C, Laland KN, Reader SM, 2001. Interactions between shoal size and conformity in guppy social foraging. *Anim Behav* 62:917–925.
- Fretwell SD, Lucas JHJ, 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor* 19:16–36.
- Galef BG Jr, Giraldeau L-A, 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim Behav* 61:3–15.
- Giraldeau L-A, Valone TJ, Templeton JJ, 2002. Potential disadvantages of using socially-acquired information. *Phil Trans R Soc Lond B* 357:1559–1566.
- Gotceitas V, Colgan P, 1991. Assessment of patch profitability and ideal free distribution: the significance of sampling. *Behaviour* 119:65–76.
- Hoare DJ, Couzin ID, Godin J-CJ, Krause J, 2004. Context-dependent group size choice in fish. *Anim Behav* 67:155–164.
- Honkanen T, Ekstrom P, 1992. Comparative study of the olfactory epithelium of the three-spined stickleback (*Gasterosteus aculeatus*) and the nine-spined stickleback (*Pungitius pungitius*). *Cell Tissue Res* 269:267–273.
- Hung AA, Plott CR, 2001. Informational cascades: replication and an extension to majority rule and conformity rewarding institutions. *Am Econ Rev* 91:1508–1520.
- Keenleyside MHA, 1955. Some aspects of the schooling behaviour of fish. *Behaviour* 8:183–248.
- Kendal RL, Coolen I, van Bergen Y, Laland KN, in press. Trade-offs in the adaptive use of social and asocial learning. *Adv Stud Behav*.
- Krause J, 1992. Ideal free distribution and the mechanism of patch profitability assessment in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behaviour* 123:27–37.
- Laland KN, Williams K, 1998. Social transmission of maladaptive information in the guppy. *Behav Ecol* 9:493–499.
- Lima SL, 1994. Collective detection of predatory attack by birds in the absence of alarm signals. *J Avian Biol* 25:319–326.
- Lima SL, 1995. Collective detection of predatory attack by social foragers: fraught with ambiguity? *Anim Behav* 50:1097–1108.
- McGregor PK, Peake TM, Lampe HM, 2001. Fighting fish *Betta splendens* extract relative information from apparent interactions: what happens when what you see is not what you get. *Anim Behav* 62:1059–1065.
- Mikheev VN, Andreev OA, 1993. Two-phase exploration of a novel environment in the guppy, *Poecilia reticulata*. *J Fish Biol* 42:375–383.
- Nordell SE, Valone TJ, 1998. Mate choice copying as public information. *Ecol Lett* 1:74–76.
- Pomiankowski A, 1990. How to find the top male? *Nature* 347: 616–617.
- Pongrácz P, Miklósi A, Kubinyi E, Topál J, Csányi V, 2003. Interaction between individual experience and social learning in dogs. *Anim Behav* 65:595–603.
- Potvin C, Roff DA, 1993. Distribution-free and robust statistical methods: viable alternatives to parametric statistics? *Ecology* 74: 1617–1628.
- Schlupp I, Marler C, Ryan MJ, 1994. Benefit to male sailfin mollies of mating with heterospecific females. *Science* 263:373–374.
- Smith JW, Benkman CW, Coffey K, 1999. The use and misuse of public information by foraging red crossbills. *Behav Ecol* 10:54–62.
- Smith RD, Ruxton GD, Cresswell W, 2001. Patch choice decisions of wild blackbirds: the role of preharvest public information. *Anim Behav* 61:1113–1124.
- Templeton JJ, 1998. Learning from others' mistakes: a paradox revisited. *Anim Behav* 55:79–85.
- Templeton JJ, Giraldeau L-A, 1995. Public information cues affect the scrounging decisions of starlings. *Anim Behav* 49:1617–1626.
- Templeton JJ, Giraldeau L-A, 1996. Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. *Behav Ecol Sociobiol* 38:105–114.
- Tinbergen N, 1951. *The study of instinct*. Oxford: Oxford University Press.
- Valone TJ, Giraldeau L-A, 1993. Patch estimation by group foragers: what information is used? *Anim Behav* 45:721–728.
- Valone TJ, Templeton JJ, 2002. Public information for the assessment of quality: a widespread social phenomenon. *Phil Trans R Soc Lond B* 357:1549–1557.
- van Bergen Y, 2004. An investigation into the adaptive use of social and asocial information (PhD dissertation). Cambridge: Cambridge University.
- van Bergen Y, Coolen I, Laland KN, 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proc R Soc Lond B* 271:957–962.
- Witte K, Massmann R, 2003. Female sailfin mollies, *Poecilia latipinna*, remember males and copy the choice of others after 1 day. *Anim Behav* 65:1151–1159.
- Witte K, Nolte, 2002. The role of information in mate-choice copying in female sailfin mollies *Poecilia latipinna*. *Behav Ecol Sociobiol* 52:194–202.