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Nine-spined sticklebacks exploit the most reliable source when public and private information conflict

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Social foragers can potentially use private information gained from personal experience and public information gained from observing the foraging success of others to determine the profitability of a foraging patch. We investigated how nine-spined sticklebacks use conflicting public and private information of variable reliability to make foraging decisions. In a first experiment, when private information was reliable, sticklebacks ignored public information and based their foraging decision on private information. However, when private information was less reliable, sticklebacks tended to use public rather than private information. A second experiment investigated how the time since experiencing private information affected sticklebacks' use of this information when it conflicted with recent public information. Fish based their foraging decisions on recently acquired private information, but reliance on private information diminished as the period since experiencing it increased. Fish used public information if 7 days had elapsed since updating their private information. Our findings suggest that nine-spined sticklebacks flexibly adjust their decision making to exploit the most reliable information available, be it public or private, and that animals will weight private and public information appropriately depending on circumstances.

Keywords: nine-spined stickleback; decision making; public information; optimal foraging theory; patch assessment; social learning

1. INTRODUCTION

To forage efficiently animals need accurate information about the quality of foraging patches. While all foragers can use private information derived from prior sampling experiences, social foragers can potentially use the behaviour of others as an additional source of information (Galef & Giraldeau 2001; Brown & Laland 2003). Public information, which refers to the ability to assess the profitability of a resource by observing the success (or lack of success) of other individuals, could lead to faster, more accurate assessment of a resource than can using private information alone (Valone 1989; Templeton & Giraldeau 1996; Valone & Templeton 2002). Combining these sources of information flexibly is potentially the optimal basis for adaptive decision making. However, assumptions about how animals gather and exploit these different types of information have generally not been tested explicitly.

Although public-information theory assumes that public information is simply another form of sample information and that both types of information ('public and private' or 'public and sample') are weighted equally (Clark & Mangel 1984; Valone 1989; Valone & Giraldeau 1993; Templeton & Giraldeau 1996), Valone & Templeton (2002) state that this is unlikely. Some types of information are conceivably more reliable (e.g. more consistent or more recent) than other types, and animals may benefit from weighting reliable information more heavily. Recent work highlights this current interest in the interplay between personal and social information in decision-making processes. For example, Nordell & Valone (1998) argue that individuals should rely on private information when they can discriminate the relative quality of two potential mates but should copy the mate choice of another individual (public information) when they cannot.

The costs associated with gathering information also need to be considered (Boyd & Richerson 1985). If accurate private information can be acquired easily and at low cost, an individual may benefit by ignoring public information (Templeton & Giraldeau 1996). Consistent with this, Day *et al.* (2004) report that guppies (*Poecilia reticulata*) with personal knowledge about which of two foraging locations contains food ignore the conflicting social information provided by foraging conspecifics unless the use of their personal knowledge inflicts costs such as breaking visual contact with the shoal. Reliance on social information can lead to arbitrary and even maladaptive traditions in animals (Laland & Williams 1998; Giraldeau *et al.* 2002; Pongrácz *et al.* 2003). However, current theoretical work suggests that, even if the costs of misinformation are high, animals should still use information, provided that its reliability is high (Koops 2004). By focusing on the potential costs associated with using different types of information, these studies illustrate the importance of correctly assessing the reliability of personal versus social information.

Previous work in our laboratory has established that nine-spined sticklebacks (*Pungitius pungitius*) are able to exploit public information from other foragers to guide their own foraging decisions (Coolen *et al.* 2003). In the present study, we investigate how nine-spined sticklebacks use information to make foraging decisions by providing an individual fish with conflicting public and private information about the relative profitability of two foraging patches. Assuming that individuals want to exploit the

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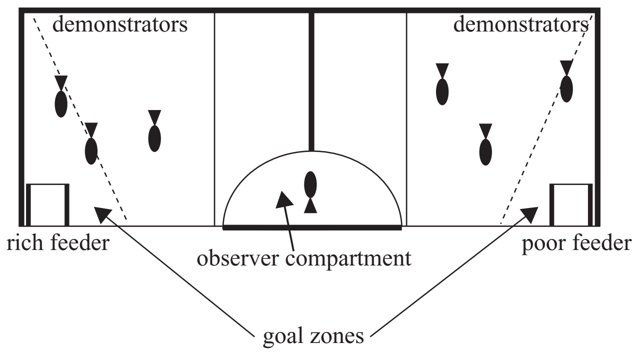

Figure 1. Diagram of the experimental apparatus for the public demonstration periods. Thick lines represent opaque partitions, thin lines represent transparent partitions and dashed lines represent goal-zone delimitations.

richer patch, the foraging-patch decision of each fish reflects which information it used. In a first experiment, groups of fish were provided with private information with different levels of reliability, followed by conflicting public information. If fish weight public and private information equally, they should exhibit no patch preference. However, if fish weight the two types of information according to their reliability, then we would expect fish to use private information when its reliability is high but not when it is low.

In a second experiment, we investigated whether nine-spined sticklebacks weight recent information differently from older, potentially outdated information. Fish were provided with reliable private information and different groups were then presented with conflicting public information 1, 3, 5 or 7 days after last updating their private information. If fish weight different sources of information depending on how recently they were obtained, they should rely on private information only if relatively little time has elapsed since it was acquired, and switch to weighting current public information more heavily after a greater time has elapsed.

2. EXPERIMENT 1: EFFECT OF RELIABILITY OF PRIVATE INFORMATION ON PATCH CHOICE

(a) *Methods*

In this experiment, we used 96 adult nine-spined sticklebacks caught from a stream in Histon, near Cambridge, UK. The fish were housed in tanks at a water temperature of 8–12 °C at the Sub-Department of Animal Behaviour, Madingley, UK, and fed on frozen bloodworms for two weeks before the experiments. Experiments were conducted between September 2002 and February 2003, outside the breeding season to minimize reproductive behaviour. Fish were deprived of food for 24 h before testing.

(i) *Private-information training sessions*

An experimental tank (30 cm × 90 cm, 18 cm water level) was established, with black plastic covering the outside of three sides of the tank (see figure 1). Two transparent partitions divided the tank into three equal sections, with a feeder placed at each end of the tank. Feeders consisted of columns (5 cm × 5 cm × 35 cm high) with opaque sides and a transparent front and back. Defrosted bloodworms, with water, were delivered at the top of each feeder by pipette. One feeder was designated 'rich' and the other 'poor' at random, and this designation was maintained throughout training. 'Rich' feeders provided three bloodworms six times in 10 min (every 90 s), while 'poor' feeders delivered three bloodworms twice in 10 min (at 1 min 30 s and 6 min). 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 odour cues.

For training sessions, shoals of fish were placed in the end sections containing the feeders and the central section was left empty. This ensured that each shoal could access only one feeder throughout each 10 min training session while still having visual access to the other feeder. This set-up 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 patches.

Six groups of 16 fish were given three training sessions a day over 6 days. Each group was split into two shoals of eight fish, one shoal in each end section. For groups 1 and 2 (56% reliable private information) each shoal was moved into the end section containing the 'rich' feeder for 10 out of 18 sessions and moved to the end section containing the 'poor' feeder for the other eight sessions; for groups 3 and 4 (78% reliable private information) each shoal was moved into the end section containing the 'rich' feeder for 14 out of 18 sessions and moved to the end section containing the 'poor' feeder for the other four sessions. These numbers were chosen to represent unreliable and fairly reliable information, within the constraints of the training set-up, which required an even number of sessions since each group was split into two shoals. The groups were counterbalanced and sessions were spread randomly over the 6 days so that the fish could not learn a pattern regarding which feeder was 'rich' on each day. For groups 5 and 6 (100% reliable private information) one feeder was consistently 'rich' for all 18 sessions.

To reduce exploratory behaviour during testing each group was left in the experimental tank overnight after the last day of private training, so that the fish were familiar with the tank devoid of partitions. Feeders were not present during this time.

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

On day 7, fish were tested 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 partitions were then removed, revealing the feeders in the same locations as during the private-information training sessions, but no food was provided. The location of the focal fish was recorded every 6 s for 5 min. Any fish exhibiting freezing behaviour 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. All other fish participated in the remainder of the experiment, regardless of which goal zone they entered first.

(iii) *Public demonstration*

On day 7, after the first preference test, each fish ($n = 20$ for 56% and 78% reliable information, $n = 23$ for 100% reliable information) experienced a public demonstration that conflicted with their private information. In this demonstration, the 'rich' feeder was that which had been 'poor' for the majority of that group's private training sessions.

A focal fish (the observer) was placed in a semicircular compartment in the middle of the experimental tank, and partitions were placed as shown in figure 1. Two groups of demonstrators, each consisting of three 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.

Each demonstration lasted 10 min, with the same feeding regime as the private-information training sessions. 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 and success to determine the profitability of each patch. Nine-spined sticklebacks are able to choose the 'rich' feeder after a single public demonstration (Coolen *et al.* 2003).

(iv) *Preference test after public demonstration*

After the public demonstration, the demonstrators and any remaining worms were removed from the experimental tank. 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 for 90 s after it left the central section of the tank or until it entered a goal zone (see figure 1), whichever happened last. A fish was considered to be in a zone if its body up to the pectoral fins was in that zone. The experimenter (Y.v.B.) was under a black plastic hide fastened to the front of the tank, designed so that objects or events outside the tank would not distract the fish. No food was provided during the preference test.

(v) *Data collection and analysis*

The feeder preference was defined as the first goal zone that each fish entered during the preference test. The proportion of fish that chose the feeder that was 'rich' according to private information first was compared with random expectations, both after private-information training and after the public demonstration. To test for sampling behaviour, the number of fish visiting both feeders in the first 90 s of the preference test after public demonstration was compared between conditions (100%, 78% and 56% reliable private information). We also compared the median amounts of time that fish in each condition spent in each goal zone during the first 90 s after the fish left the central section of the tank.

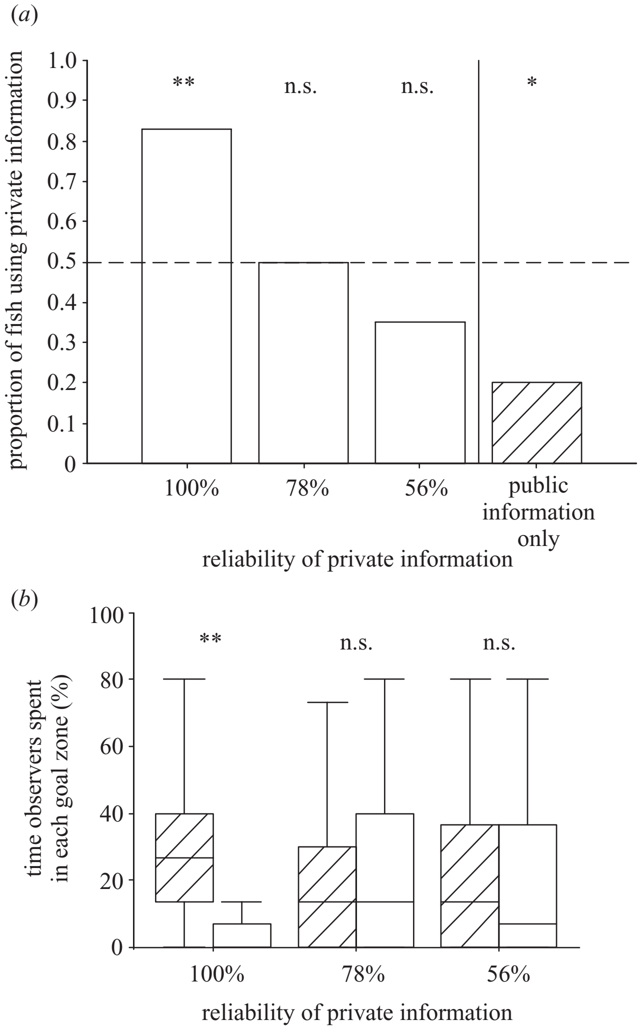

Figure 2. Observers' behaviour after receiving private information of variable reliability followed by conflicting public information. (*a*) Proportion of observers entering the goal zone of the feeder that was 'rich' according to private information first. The dashed line indicates the proportion expected at random. Data represented by the hatched bar are from Coolen *et al.* (2003). (*b*) Median ($\pm$ interquartile range and maximum and minimum values) percentages of time observers spent in each goal zone (private-information goal zone, hatched bars; public-information goal zone, unfilled bars) in the first 90 s after leaving the central section of the tank; $^{*}p < 0.05$, $^{**}p < 0.005$.

(b) *Results*

(i) *Preference test after private training*

After the private training, a significant majority of fish with 100% reliable private information first visited the feeder that was 'rich' according to private information ($\chi^2 = 9.78$, d.f. = 1, $p < 0.005$, Bonferroni $\alpha^* = 0.025$). The preference of fish with 78% reliable information approached significance ($\chi^2 = 3.2$, d.f. = 1, $p = 0.07$; $\alpha^* = 0.025$). Fish with 56% reliable private information did not show a preference for either feeder ($\chi^2 = 1.8$, d.f. = 1, $p = 0.2$; $\alpha^* = 0.025$).

(ii) *Preference test after public demonstration*

The proportion of fish using private information after the public demonstration differed significantly between conditions ($\chi^2 = 10.5$, d.f. = 2, $p = 0.005$). A significant majority of fish with 100% reliable private information (19 out of the 23 tested fish) first visited the feeder that was 'rich' according to private information ($\chi^2 = 9.78$, d.f. = 1, $p < 0.005$; figure 2*a*). Fish with 78% or 56% reliable private information showed no preference (78%: 10 out of 20 fish first visited the feeder that was 'rich' according to private information, $\chi^2 = 0$, d.f. = 1, $p = 1$; 56%: seven out of 20 fish first visited the feeder that was 'rich' according to private information, $\chi^2 = 1.8$, d.f. = 1, $p = 0.18$; figure 2*a*). The number of fish sampling both feeders during the first 90 s of the test did not differ between conditions ($\chi^2 = 0.88$, d.f. = 2, $p = 0.65$). For 100% and 78% reliable private information, the feeder preference of the fish after the public demonstration did not differ from their feeder preference immediately after private training (100%: $\chi^2 = 0$, d.f. = 1, $p = 1$; 78%: $\chi^2 = 3.2$, d.f. = 1, $p = 0.07$; $\alpha^* = 0.025$). However, a significant proportion of fish with 56% reliable private information switched to using public information after the public demonstration ($\chi^2 = 7.9$, d.f. = 1, $p < 0.005$; $\alpha^* = 0.025$).

(iii) *Time spent in goal zones after public demonstration*

Fish with 100% reliable private information spent significantly more time in the goal zone of the feeder that was 'rich' according to private information than in the goal zone of the feeder that was 'rich' according to public information (Wilcoxon: $Z = -2.96$, $p < 0.005$; figure 2*b*). Fish with 78% or 56% reliable private information showed no preference (Wilcoxon: 78%: $Z = -0.24$, $p = 0.81$; 56%: $Z = -0.16$, $p = 0.87$; figure 2*b*). The time spent in each goal zone did not differ between conditions (public goal zone: Kruskal–Wallis: $\chi^2 = 3.89$, d.f. = 2, $p = 0.14$; private goal zone: Kruskal–Wallis: $\chi^2 = 3.41$, d.f. = 2, $p = 0.18$). The amount of time spent in the private goal zone did not gradually decrease with decreasing reliability of private information (Jonckheere–Terpstra trend test: J–T statistic = −1.55, $p = 0.12$), and there was no corresponding increase in the time spent in the public goal zone (Jonckheere–Terpstra trend test: J–T statistic = 1.69, $p = 0.09$).

(iv) *Comparison with public information only*

Coolen *et al.* (2003) employed an identical public-demonstration procedure and apparatus, but their fish had no prior private information. As a further test of whether fish remembered private information here, the proportion of fish using public information in the present study was compared with the proportion of fish using public information in Coolen *et al.* (2003). If fish have forgotten their private information, their foraging decisions should not differ from those of fish that have only public information. Significantly fewer fish with 100% or 78% reliable private information used public information than did fish that had only public information (100%: $\chi^2 = 56.4$, d.f. = 1, $p < 0.005$; 78%: $\chi^2 = 11.3$, d.f. = 1, $p < 0.005$; $\alpha^* = 0.017$), but the preference of fish with 56% reliable private information did not differ from that of fish that had only public information ($\chi^2 = 2.8$, d.f. = 1, $p = 0.1$; $\alpha^* = 0.017$).

(c) *Discussion*

Only fish with 100% reliable private information preferred the feeder that was 'rich' according to private information and spent more time near it than near the other feeder. Fish with 78% or 56% reliable private information did not exhibit a clear preference for private or public information. Neither did fish with 78% or 56% reliable private information resolve the conflict between public and private information by gathering sample information during the test. On average, fish with less reliable information spent equal amounts of time in both goal zones only because half of the fish used public information and the other half used private information.

Only fish with 100% reliable private information appeared to use this information after the private-information training sessions. The fact that fish with 56% reliable private information switched to using public information after the public demonstration, combined with the fact that their decisions did not differ from those of fish with public information alone, suggests that these fish never acquired private information. However, fish with 78% reliable information did not switch to using public information and their decisions differed significantly from those of fish with public information alone, suggesting that private information was present and influenced the decisions of fish with 78% reliable information.

These findings suggest that sticklebacks will favour private over public information if they have completely reliable private information but not when this information is unreliable. The next experiment investigated whether sticklebacks still use reliable private information if it has not been updated recently.

3. EXPERIMENT 2: EFFECT OF LATENCY BETWEEN PRIVATE AND PUBLIC INFORMATION ON PATCH CHOICE

(a) *Methods*

In this experiment, we used 100 nine-spined sticklebacks caught from the same stream and housed in the same conditions as those in Experiment 1.

(i) *Private-information training sessions*

Fish were provided with 100% reliable private information about relative patch quality, using the same procedure as in Experiment 1. Two shoals of 10 fish were moved to the experimental tank for each training session. All fish received three sessions per day over 6 days, during which the same feeder was always 'rich'.

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

On day 7, fish were tested individually for a feeder preference using the same procedure as in Experiment 1. Only fish that entered the 'rich' goal zone before the 'poor' goal zone within 5 min (87 fish) took part in the remainder of the experiment.

(iii) *Public demonstration*

Fish that preferred the 'rich' goal zone during the preference test were then given a public demonstration in which the 'rich' feeder was the opposite of that in the private-information training sessions, using the same procedure as in Experiment 1. One group of 23 fish was given a public demonstration 1 day after the last private-information training session, a second group (22 fish) 3 days after training, a third group (20 fish) 5 days after training and a fourth group (22 fish) 7 days after training.

(iv) *Preference test after public demonstration*

Immediately after the public demonstration, each fish was tested for a feeder preference, using the same procedure as in Experiment 1.

(b) *Results*

(i) *Preference test after public demonstration*

The proportion of fish using private information differed significantly between groups ($\chi^2 = 19.2$, d.f. = 3, $p < 0.005$). One day after private-information training, the majority of fish (19 out of the 23 tested fish) first visited the feeder that was 'rich' according to private information ($\chi^2 = 9.78$, d.f. = 1, $p < 0.005$; figure 3*a*). Fish in groups with delays of 3 or 5 days showed no

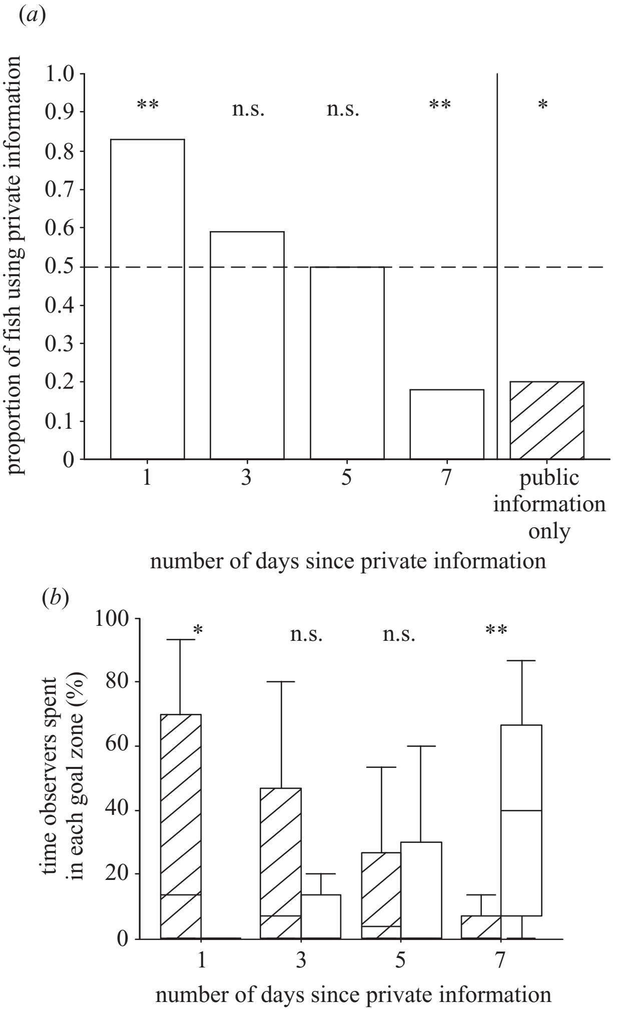

Figure 3. Observers' behaviour after receiving entirely reliable private information followed by conflicting public information 1, 3, 5 and 7 days later. (*a*) Proportion of observers entering the goal zone of the feeder that was 'rich' according to private information first. The dashed line indicates the proportion expected at random. Data represented by the hatched bar are from Coolen *et al.* (2003). (*b*) Median (± interquartile range and maximum and minimum values) percentage of time observers spent in each goal zone (private-information goal zone, hatched bars; public-information goal zone, unfilled bars) in the first 90 s after leaving the central section of the tank; $^{*}p < 0.05$, $^{**}p < 0.005$.

preference for either feeder (3 days: 13 out of 22 fish first visited the feeder that was 'rich' according to private information, $\chi^2 = 0.73$, d.f. = 1, $p = 0.39$; 5 days: 10 out of 20 fish first visited the feeder that was 'rich' according to private information, $\chi^2 = 0$, d.f. = 1, $p = 1$; figure 3*a*). By contrast, the majority of fish (18 out of 22) in the group with a delay of 7 days first visited the feeder that was 'rich' according to public information ($\chi^2 = 8.91$, d.f. = 1, $p < 0.005$; figure 3*a*). The number of fish sampling both feeders did not differ between groups ($\chi^2 = 0.43$, d.f. = 3, $p = 0.93$).

(ii) *Time spent in goal zones after public demonstration*

One day after private-information training fish spent significantly more time in the goal zone of the feeder that was 'rich' according to private information than in the goal zone of the feeder that was 'rich' according to public information (Wilcoxon: $Z = -2.48$, $p < 0.05$; figure 3*b*). After a delay of 3 days there was still a strong tendency, though not quite significant, to spend more time in the private-information goal zone (Wilcoxon: $Z = -1.94$, $p = 0.052$), but by day 5 fish did not prefer either goal zone (Wilcoxon: $Z = -0.48$, $p = 0.64$; figure 3*b*). Fish in the group with a delay of 7 days spent more time near the feeder that was 'rich' during the public demonstration (Wilcoxon: $Z = -3.17$, $p < 0.005$; figure 3*b*). The amount of time spent in the private-information goal zone tended to differ between groups (Kruskal–Wallis: $\chi^2 = 7.39$, d.f. = 3, $p = 0.06$), decreasing as the delay between private and public demonstrations increased (Jonckheere–Terpstra trend test: J–T statistic = -2.72, $p < 0.01$). The amount of time spent in the public-information goal zone differed between conditions (Kruskal–Wallis: $\chi^2 = 25.9$, d.f. = 3, $p < 0.005$), increasing similarly (Jonckheere–Terpstra trend test: J–T statistic = 5.03, $p < 0.005$).

(iii) *Comparison with public information only*

Significantly fewer fish in groups with delays of 1, 3 or 5 days used public information than did fish in Coolen *et al.* (2003), which had only public information (1 day: $\chi^2 = 56.4$, d.f. = 1, $p < 0.005$; 3 days: $\chi^2 = 21.0$, d.f. = 1, $p < 0.005$; 5 days: $\chi^2 = 11.3$, d.f. = 1, $p < 0.005$; $\alpha^* = 0.0125$). The feeder preferences of fish with a delay of 7 days did not differ from those of fish that had only public information ($\chi^2 = 0.05$, d.f. = 1, $p = 0.8$; $\alpha^* = 0.0125$).

(c) *Discussion*

The fish did not simply rely on the most recent (here, public) information that they had obtained. On the contrary, they appeared to rely on private information 1 day after they had last updated it. However, after delays of 3 or 5 days, they no longer preferentially used private over public information, and after 7 days they relied on public information. Fish with less reliable (more likely to be outdated) private information did not increase their sampling behaviour. However, there was a gradual shift in the information that sticklebacks relied on, with fish spending increasing amounts of time in the public-information goal zone with increased time since updating their private information.

4. GENERAL DISCUSSION

The results of this study suggest that nine-spined sticklebacks weight public and private information differently, depending on circumstances, to make adaptive foraging decisions. We found that nine-spined sticklebacks ignored conflicting public information in favour of reliable private information that had been acquired recently. However, the fish ignored private information that had not been updated for 7 days in favour of recent public information. This suggests that fish exploit only public information when their private information about patch quality is old or uncertain, a finding consistent with the (hitherto untested) assumptions of theoretical models exploring the circumstances under which animals rely on social and asocial learning (Boyd & Richerson 1988). Animals may profitably adopt a social-learning strategy of 'copy when uncertain' but otherwise rely on their own personal experience (Laland 2004).

When private information was less reliable (56% or 78% reliable in Experiment 1, and after delays of 3 or 5 days in Experiment 2) approximately half of the sticklebacks seemingly used public information, whereas the other half used private information to estimate foraging-patch quality. It is perhaps surprising that fish did not resolve the conflict between private and public information by increasing their sampling behaviour, especially since sample information would not have been costly to acquire in this experimental set-up where patches were not far apart. However, we have data for only the first 90 s after the fish left the central section of the tank, and it is possible that with a longer test period we would have observed an increase in sampling. One possible explanation for the reluctance of nine-spined sticklebacks to visit both feeders is the increased predation risk of swimming between food patches in open water, particularly alone. Owing, in part, to their vulnerability to predation (Hoogland *et al.* 1957), nine-spined sticklebacks spend most of their time in vegetation (Coolen *et al.* 2003; Hart 2003) from where they may collect public information and use it to swim directly to the most profitable patch (Coolen *et al.* 2003).

Although we cannot rule out the possibility that the number of fish using private information in Experiment 2 dropped as the delay increased because the fish had forgotten their private information, we think that this explanation is unlikely. The foraging decisions of fish in this study were compared with those of fish that had only public information, and fish with both types of information (in groups with delays of 1, 3 or 5 days) were less likely to use public information than were fish with public information alone. This suggests that private information was still present and influenced the decisions of subjects in these groups. It is possible that, after a delay of 7 days, fish had forgotten their private information. However, Milinski (1994) found that three-spined sticklebacks (*Gasterosteus aculeatus*) remembered the location of a foraging patch for up to 8 days. Given that three-spined and nine-spined sticklebacks are closely related and live sympatrically (and are therefore likely to be exposed to similar rates of environmental change), we might expect three-spined and nine-spined sticklebacks to have similar levels of retention. Moreover, forgetting outdated information may be an adaptive strategy in an environment that changes frequently.

The results of the present study conflict with both empirical work and theoretical models that have assumed that foragers weight personal and social information equally (Clark & Mangel 1984; Valone 1989; Valone & Giraldeau 1993; Templeton & Giraldeau 1996). To our knowledge, Day *et al.* (2004) and the present study are the first to test this assumption empirically, and neither find evidence to support it. Whether animals exploit social information depends both on the perceived reliability of personal information and on the perceived costs of using personal information. Our understanding of individual decision-making processes in a social context will be greatly improved by studies that explicitly test assumptions about when animals should use different types of information (Laland 2004).

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