

Social learning strategies and predation risk: minnows copy only when using private information would be costly

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Animals can acquire information from the environment privately, by sampling it directly, or socially, through learning from others. Generally, private information is more accurate, but expensive to acquire, while social information is cheaper but less reliable. Accordingly, the ‘costly information hypothesis’ predicts that individuals will use private information when the costs associated with doing so are low, but that they should increasingly use social information as the costs of using private information rise. While consistent with considerable data, this theory has yet to be directly tested in a satisfactory manner. We tested this hypothesis by giving minnows (*Phoxinus phoxinus*) a choice between socially demonstrated and non-demonstrated prey patches under conditions of low, indirect and high simulated predation risk. Subjects had no experience (experiment 1) or prior private information that conflicted with the social information provided by the demonstrators (experiment 2). In both experiments, subjects spent more time in the demonstrated patch than in the non-demonstrated patch, and in experiment 1 made fewer switches between patches, when risk was high compared with when it was low. These findings are consistent with the predictions of the costly information hypothesis, and imply that minnows adopt a ‘copy-when-asocial-learning-is-costly’ learning strategy.

Keywords: social learning; cultural transmission; predation risk; fish; social learning strategy; social foraging

1. INTRODUCTION

Animals can acquire adaptive information directly, through their own asocial personal experience or through copying others. First-hand sampling allows animals to gather accurate, up to date private information about their immediate environment. Doing so can be costly, however, both in terms of the time and energy that must be invested, and also through the increased likelihood of encountering predators or exposure to other risks while gathering it. In theory, these costs can be reduced through the use of social information; by observing or interacting with others an individual can sidestep the need to sample resources directly, perhaps even gathering this information from the relative safety of cover (Zentall & Galef 1988; Feldman *et al.* 1996; Heyes & Galef 1996; Giraldeau *et al.* 2002; Laland 2004; Kendal *et al.* 2005; Hoppitt & Laland 2008).

The disadvantage of relying solely upon social information is that it is potentially less reliable than privately gathered information. Copying errors can render social information inaccurate, while the transmission of information between individuals can lead to the accumulation of errors and the formation of cascades of misinformation. In temporally variable environments social information has the potential to become outdated or obsolete over time, while in spatially variable environments differences in local optima mean that the relative usefulness of social information will vary between sites. The use of private versus social sources of information by animals can

therefore be viewed as a trade-off between accuracy and cost. Boyd & Richerson (1985) proposed a *costly information hypothesis*, which suggests that when information is too costly to acquire or use personally, individuals will take advantage of the relatively cheaper information provided by others. Laland (2004) characterized this hypothesis as a ‘copy-when-asocial-learning-is-costly’ social learning strategy.

While Boyd and Richerson proposed their costly information hypothesis with humans in mind, in principle the same reasoning should apply to other animals capable of social learning. However, while several studies provide data that are broadly consistent with this hypothesis (Baron *et al.* 1996; Coolen *et al.* 2003; Kendal *et al.* 2004; Webster & Hart 2006), hitherto there has been only one attempt to test it directly. Galef & Whiskin (2006) found that rats (*Rattus norvegicus*) foraging in the presence of predators (cats, *Felis domesticus*) did not use social information to a greater extent when selecting between demonstrated and non-demonstrated food types than rats tested in the absence of predators. This finding is contrary to the predictions of the copy-when-asocial-learning-is-costly strategy favoured by the costly information hypothesis, and is difficult to interpret. It is possible that the failure to support the hypothesis is an artefact of an experimental design in which the demonstrated and non-demonstrated foods were presented in the same location. Risk was incurred by the rats leaving shelter to reach the foods however, once there was no additional cost (in terms of predation risk, at least) associated with choosing the non-demonstrated food.

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In this study, we again attempt a direct test of the copy-when-asocial-learning-is-costly strategy, but here the two options that subjects choose between are spatially segregated, and thereby allow the subjects to attribute different potential costs to the alternatives. European minnows (*Phoxinus phoxinus*), a shoaling fish, were presented with a choice of foraging at two different food sites, in separate locations, under differing levels of simulated predation risk. Focal fish, confined in a shelter, were first allowed to observe the two feeders, representing discrete prey patches. One feeder had a small group of conspecific demonstrators held in attendance, while the other did not. Following this demonstration period the conspecifics were removed, and the focal individual was allowed to leave the shelter and forage, under one of three treatments: (i) low risk, where cover was available and no predator stimulus was present, (ii) indirect risk, where no predator stimulus was present, but where cover was now absent, and (iii) high risk, where cover was absent and model predators were present. Since, at test, no demonstrators are present, selection of the demonstrated feeder is an indicative of social learning.

We performed two experiments. In the first experiment, the focal fish had prior experience of feeding from the feeders, but no private information about the quality of either of the two feeders in the experimental situation. In the second experiment, the focal fish had prior private information that one feeder contained prey, while the other did not. During the observation phase of the experiment, subjects received conflicting social information from the demonstrators who were confined within the area of the feeder that the focal fish had previously experienced to be empty. In both cases, after the demonstration phase, subjects were tested to see whether they exploited the socially demonstrated feeder to a greater extent than the alternative, and whether such use of social information increased with predation risk. We predicted that the focal fish in the high-risk treatment would use social information to a greater extent than those in the indirect-risk treatment, who would in turn use social information more than subjects in the low-risk treatment. Specifically, we predicted that with increasing simulated predation risk, subjects would (i) spend more time in the vicinity of the demonstrated feeder and less time at the alternative feeder and (ii) switch between feeders to a lesser extent. Such behaviour would provide the first experimental confirmation of the costly information hypothesis in a non-human animal, and imply that minnows adopt a copy-when-asocial-learning-is-costly foraging strategy.

2. MATERIAL AND METHODS

(a) Subjects

Juvenile minnows were collected from Clow Beck, North Yorkshire, UK (54°29'08" N, 1°38'43" W), using dip nets in October 2007. The minnows in Clow Beck co-occur with a number of predatory fishes (brown trout, *Salmo trutta*; chub, *Leuciscus cephalus*; Eurasian perch, *Perca fluviatilis*; and northern pike, *Esox lucius*) and birds (grey heron, *Ardea cinerea*; kingfisher, *Alcedo atthis*) and are therefore likely to be subjected to intense predation pressure. Captured minnows were taken to the laboratory where they were housed in groups of 20 in 45 l aquaria. Each aquarium contained an

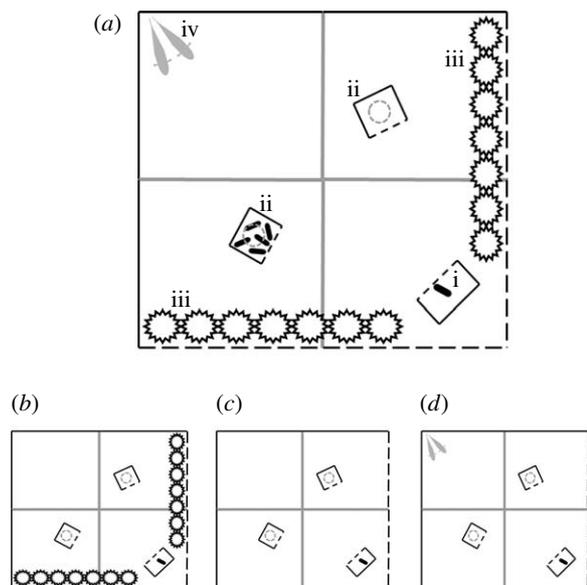


Figure 1. (a) The test tank, configured for (b) low-, (c) indirect- and (d) direct-predation risk treatments. Here (i) is a perspex start box shelter, (ii) are stimulus chambers, simulating food patches, (iii) is cover, in the form of artificial vegetation, and (iv) shows the location of two model predators. Further details are given in the main text. Diagrams are not drawn to scale.

internal filter, and artificial vegetation for cover. The light:dark regime was held at 12:12 hours and the temperature was maintained at 8°C. They were fed daily with a mixture of commercial flake food and freeze-dried bloodworms and daphnia. They were held under these conditions for five months, with the experiments taking place between February and May 2008, by which time they measured 30–35 mm in length.

(b) Apparatus and procedure

Six weeks prior to the start of the experiments, we began to introduce food, freeze-dried bloodworms, into the housing tanks in yellow plastic feeding rings (hereafter: feeders) (1 cm deep, 4 cm diameter) floated on the water surface. One yellow feeder was added to each aquarium at feeding time, with food placed in its centre, and the fish were allowed to feed from it. At the same time, a blue feeder was added to the tank. This feeder never contained food. Similar feeders were later used in the experiments, and this procedure served to train the fish to associate them with food, in the case of the yellow feeders, or no food, in the case of the blue ones. Twenty minutes after the food was provided both feeders were removed. At the end of this procedure, fish would immediately approach the yellow feeders but ignored the blue ones.

Fish were tested in the experimental tank shown in figure 1a. The experimental tank was divided into four quadrants: the starting quadrant; the demonstrated and non-demonstrated goal zone quadrants that contained the feeders; and the predator stimulus quadrant. The tank measured 75 cm square by 18 cm deep, with a water depth of 12 cm. Two sides of the tank were covered with opaque black plastic (figure 1, solid lines) and the other two with one-way film (Purlfrost Ltd, London, UK; figure 1, dashed lines). One quadrant housed a black Perspex start box shelter ((i) in figure 1a) measuring 12 cm wide by 6 cm long and 6 cm deep. This was raised on legs 6 cm from the base of the test tank so that its roof was at the water surface. The roof was removable,

as was the front wall, which was constructed from clear Perspex and set in grooves in the side walls allowing it to be raised vertically and removed. At the beginning of a trial, the front wall was set in place and the focal fish was added, and sealed in by placing the roof on top. To start the trial, the front wall could be slid up and removed. Two other quadrants housed stimulus chambers ((ii) in figure 1*a*) measuring 12 by 12 cm by 20 cm tall. The sides, rears and bases of these were constructed from black Perspex, and the fronts, which faced towards the start box, were constructed from transparent Perspex. The stimulus chambers were watertight, so that no exchange of water between the stimulus chambers and the main tank could occur, and were filled to 12 cm depth. Each stimulus chamber contained a feeder (4 cm diameter, 1 cm tall) floating on its surface. One stimulus chamber contained a shoal of five demonstrator fish, while the other remained empty. The quadrants housing these were, respectively, designated the demonstrated and non-demonstrated goal zones. Cover ((iii) in figure 1*a*), in the form of 50 cm long, by 5 cm wide rows of artificial vegetation was provided in the test tank along the walls leading away from the start box. Two artificial predators ((iv) in figure 1*a*), 10 cm long realistic models of perch (*Perca* sp., manufactured by Storm Naturalistic Inc.), were present in the high-predation risk treatment only. These were suspended 6 cm apart from one another, 4 cm from the base of the tank and 10 cm from the corner of the quadrant directly opposite to the start box. Model predators were absent during the demonstration phase for all three treatments.

The conditions during the test phase were as follows. In the low-risk treatment, the cover along the sides of the test tank was retained, providing the fish with ready access to shelter as it moved about the tank. No predator stimulus was present (figure 1*b*). The term 'low risk' is a relative one, since the combination of being alone and in a novel environment is designed to have induced some mild stress in the focal fish. For the indirect-risk treatment, the cover was removed (figure 1*c*). While no predators were present, the lack of cover was designed to mimic natural circumstances that would increase the likelihood of being captured should a predator appear while the fish was in the open. For the high-risk treatment, the cover was also removed and the model predators added (figure 1*d*).

Prior to the start of the experiments, all focal fish and demonstrators were deprived of food for 24 hours to ensure the motivation to feed. Demonstrators were drawn from a pool of approximately 50 fish. No individual was used as a demonstrator more than once in any 2 day period during the study and no focal fish was used more than once at any point.

The trial began with the addition of a group of five demonstrators to one stimulus chamber and allowed to settle for 2 min. The positioning of the demonstrator group was alternated between trials. The stimulus chambers were watertight, preventing alarm substance (Schreckstoff, Von Frisch 1938) or other chemical cues that might affect the behaviour of the focal fish from entering the main test tank. The focal fish was then added to the start box shelter, where it was allowed to settle and observe the feeders and demonstrator shoal for a further 10 min. No food was present and the presence or absence of conspecifics was the only cue concerning patch quality available to the focal fish.

After this demonstration period, a black Perspex screen was placed in front of the start box shelter, preventing the focal fish from seeing into the main tank. The stimulus chambers,

and the demonstrators and feeders within them were then removed, and were replaced with identical feeders mounted on 12 cm tall, 1 cm wide stands, which held them at the surface and prevented them from drifting around the tank.

The experimental tank was then reconfigured according to the condition (see above), which took approximately 30 s, after which the black screen was removed. The focal fish was allowed to settle for two further minutes before the sliding front door of the start box shelter was raised and removed, beginning the trial. No food was presented at test, to ensure that the subjects' patch choices were unbiased by information that could be directly gauged from the start box, such as visual or olfactory cues. This meant that the focal fish had only two sources of information about the food patches: their own prior experience of having fed from the feeders, and prior experience of having seen demonstrators gathered beneath one of them. Previous research by our group has shown this type of choice assay to be highly effective (e.g. Coolen *et al.* 2003, 2005; Van Bergen *et al.* 2004).

We recorded the latency of the focal fish to emerge from the start box shelter. Once the fish had fully emerged, we point-sampled its location by noting which quadrant it occupied at 20 s intervals, for a further 10 min ($n=30$ recordings). Pilot observations revealed that a fish could cross the tank in less than 10 s at its normal cruising speed, suggesting that a sampling time of 20 s was easily sufficient to ensure that the location of a fish at time t_2 was not dependent on its position at time t_1 . Ten minutes was chosen for the trial duration (post-emergence from the start box) since this period of time was sufficient for the fish to make several inspections of each feeder, without being so long that the fish habituated to either the model predators or to the lack of food in the feeders. We also noted which goal quadrant the subject entered first and the number of switches between goal quadrants that it made. We defined a switch as occurring when a fish left one goal quadrant and entered any other quadrant, before re-entering one of the goal quadrants. No fish re-entered the start box after emerging from it, although many returned to shelter beneath it. These were recorded as being in the starting quadrant. Where fish straddled the line between two quadrants, we used the location of its head to decide which it was occupying. After each trial the water in the experimental tank was replaced.

(c) Statistical analyses

The time to emerge and switching rates of focal fish were compared between treatment groups within each experiment using a one-way ANOVA with Tukey's HSD *post hoc* analyses. For each fish, the number of point samples in which it occurred in the non-demonstrated goal quadrant were subtracted from the number in which it was recorded in the demonstrated goal quadrant. These difference values were then compared between treatment groups using a one-way ANOVA with Tukey's HSD *post hoc* analyses. We compared the total time spent in both goal quadrants between the three treatments using a one-way ANOVA, in order to determine whether total time spent in the vicinity of either prey patch changed as a function of increasing simulated predation risk. Data were normalized using arcsine transformations where appropriate. Within each treatment group, we also compared these difference values (time in the demonstrated goal quadrant – time in the non-demonstrated goal quadrant) against a null expected value of 0 using

Wilcoxon signed-rank tests. Finally, we used binomial tests to compare the first goal quadrant choice of the focal fish within each treatment against a null expected distribution of 0.5. Focal fish that failed to enter either goal quadrant were excluded from this last analysis.

(d) *Pilot study: methods*

In order to reassure ourselves that any observed preference for the demonstrated feeders was a foraging decision, rather than merely a preference for a goal zone that previously housed conspecifics, a pilot study was conducted. The procedure was identical to the high-predation risk condition, except that no feeders were present during the demonstration phase of the experiment. Following the demonstration period, the test tank was configured to simulate high predation risk (figure 1d). If fish were attracted to the last known position of the stimulus shoal, or spent more time in that region because they are searching for it, then we should expect to see a preference for the demonstrated quadrant. Conversely, if the fish in experiment 1 were using the location of the stimulus shoal as an estimation of prey patch quality (either in terms of expected prey yield or patch safety), then we should expect to see no preference for either quadrant in the pilot study. We conducted 18 trials using previously untested fish, and recorded the goal zone entered first by the focal fish and the amount of time that it spent in each, as described above.

(e) *Pilot study: results*

Focal fish showed no preference for entering the demonstrated quadrant first; nine entered this quadrant first, compared with seven entering the non-demonstrated quadrant first, while two failed to enter either (binomial test: $n=16$, $p=0.80$). We also observed no differences in the time spent by the focal fish in the two goal zones (Wilcoxon signed-rank test: $n=18$, $Z=-0.14$, $p=0.88$). We saw no difference in the latency to emerge from shelter compared with the focal fish in the high-predation risk treatments of experiments 1 and 2 (ANOVA: $F_{2,53}=1.46$, $p=0.24$). The pilot study thus implies that any patch preference which we observe in experiment 1 is at least partly a manifestation of a foraging decision by the subjects, rather than exclusively a predator avoidance or shoaling decision.

3. EXPERIMENT 1: NO PRIOR INFORMATION

Minnows in low-, indirect- and high-risk conditions first observed demonstrator conspecifics feeding at one of two identical feeders (yellow-coloured floating feeders), and were then tested for their patch choice. Subjects had previously fed from identical feeders, but had no prior personal information as to which of the two feeders in the test environment, if either, constituted the 'better' prey patch. Fish were thus able to use either social information or private sampling to choose between the food patches. Conceivably, the presence of demonstrators at one feeder might imply that it was a richer patch, or a safer location for foraging, compared with the alternative, especially as investigating the feeders or switching between them meant leaving shelter to cross open water.

(a) *Results*

Focal fish in the high-risk treatment took a significantly longer time to emerge from the start box shelter than did fish in either the low- or indirect-risk treatments (ANOVA:

$F_{2,53}=7.45$, $p=0.001$; Tukey's HSD *post hoc* analyses: $p=0.002$ and 0.011 , respectively). We saw no differences between the low- and indirect-risk treatments (Tukey's HSD *post hoc* analyses: $p=0.83$; figure 2a).

We observed an increasing trend towards entering the demonstrated goal zone first with increasing predation risk. Binomial tests revealed that fish in the low-risk treatment were no more likely to enter the demonstrated goal quadrant than the non-demonstrated goal quadrant first (low risk: nine entered the demonstrated goal quadrant first, seven the non-demonstrated and two entered neither, $p=0.80$). For fish in the indirect-risk treatment, we observed a trend for them to enter the demonstrated goal quadrant first that approaches significance (indirect risk: 11 entered the demonstrated goal quadrant first, three the non-demonstrated and four entered neither, $p=0.057$). In the high-risk treatment, however, we saw that 17 fish entered the demonstrated goal quadrant first compared with just one entering the non-demonstrated quadrant, a difference that was strongly significant ($p=0.001$; figure 2b).

The same pattern can be observed in the time spent in the two goal zones (figure 2c). The difference in time spent in the two goal quadrants (samples recorded in the demonstrated goal quadrant—those in the non-demonstrated quadrant) was significantly greater in the high-risk treatment compared with the low-risk treatment (ANOVA: $F_{2,53}=3.32$, $p=0.034$; Tukey's HSD *post hoc* analyses: $p=0.03$). We saw no differences between the low- and indirect-risk treatments and indirect- and high-risk treatments (Tukey's HSD *post hoc* analyses: $p=0.89$ and 0.12 , respectively).

Fish in the high-risk treatment group spent more time in the demonstrated goal zone than they did in the non-demonstrated goal zone (Wilcoxon signed-rank test: $n=18$, $Z=-3.72$, $p<0.001$), while those in the low- and indirect-risk treatment groups did not ($n=18$, $Z=-0.93$, $p=0.35$ and $n=18$, $Z=-1.43$, $p=0.15$, respectively). We also saw no difference between the three treatments in the total time spent in both goal quadrants combined (ANOVA: $F_{2,53}=0.11$, $p=0.89$).

Finally, we found that fish in the high-risk treatment were significantly less likely to switch between goal quadrants when compared with the low-risk treatment group (ANOVA: $F_{2,53}=2.99$, $p=0.045$; Tukey's HSD *post hoc* analyses: $p=0.04$), with no differences between the low- and indirect-risk treatments and indirect- and high-risk treatments (Tukey's HSD *post hoc* analyses: $p=0.17$ and 0.88 , respectively; figure 2d).

4. EXPERIMENT 2: PRIOR PERSONAL INFORMATION

In the demonstration and test phases of experiment 2, individual focal fish were presented with two visually distinct food patches, in the form of different coloured feeders, one yellow and the other blue. As the fish had been given previous experience of feeding from yellow feeders, and of never finding food in blue ones, their prior personal information indicated that the patch designated by the yellow feeder was more likely to contain food. However, during the demonstration phase of the experiment, they were provided with conflicting social information, in the form of a group of demonstrators held

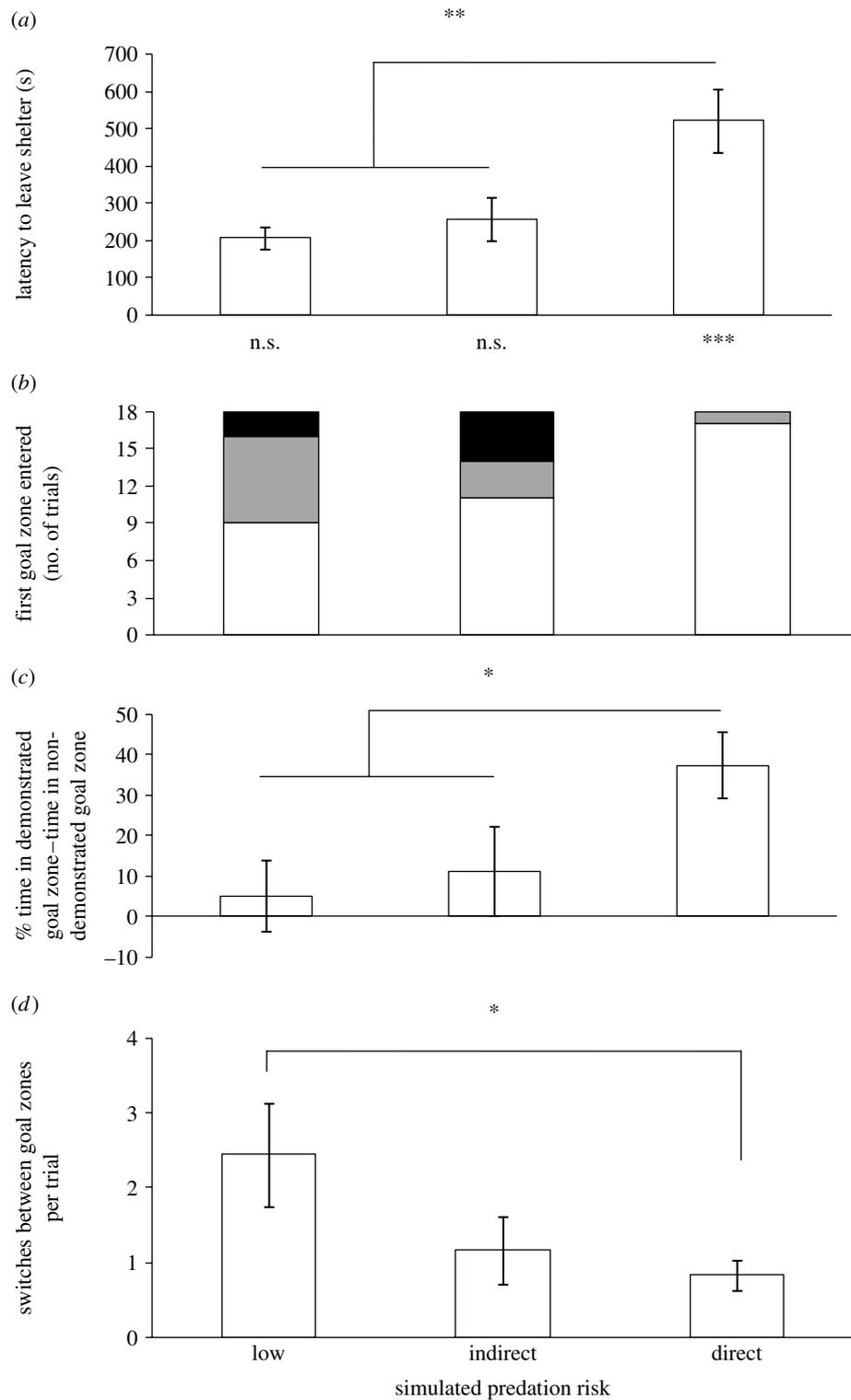


Figure 2. Experiment 1: social information versus private sampling. (a) Mean latency (\pm s.e.) of focal fish to emerge from the start box shelter. (b) The number of trials in which fish first entered the demonstrated (white) and non-demonstrated (grey) goal zones. Fish that failed to enter either are shown in black. (c) The mean difference between time spent in the demonstrated and non-demonstrated goal zones (\pm s.e.). (d) The mean number of switches (\pm s.e.) made between goal zones by the focal fish. 'n.s.', no statistically significant difference.

beneath the blue feeder, seemingly exploiting this patch. Fish in experiment 2 were able to use private information, social information or private sampling to choose between the feeders.

(a) Results

As in experiment 1, focal fish in the high-risk treatment took a significantly longer time to emerge from the start

box shelter than did fish in either the low- or indirect-risk treatments (ANOVA: $F_{2,53} = 6.63$, $p = 0.003$; Tukey's HSD *post hoc* analyses: $p = 0.009$ and 0.006 , respectively). We saw no difference between the low- and indirect-risk treatments (Tukey's HSD *post hoc* analyses: $p = 0.99$; figure 3a).

Binomial tests revealed that fish in all the three treatment groups were no more likely to enter the demonstrated

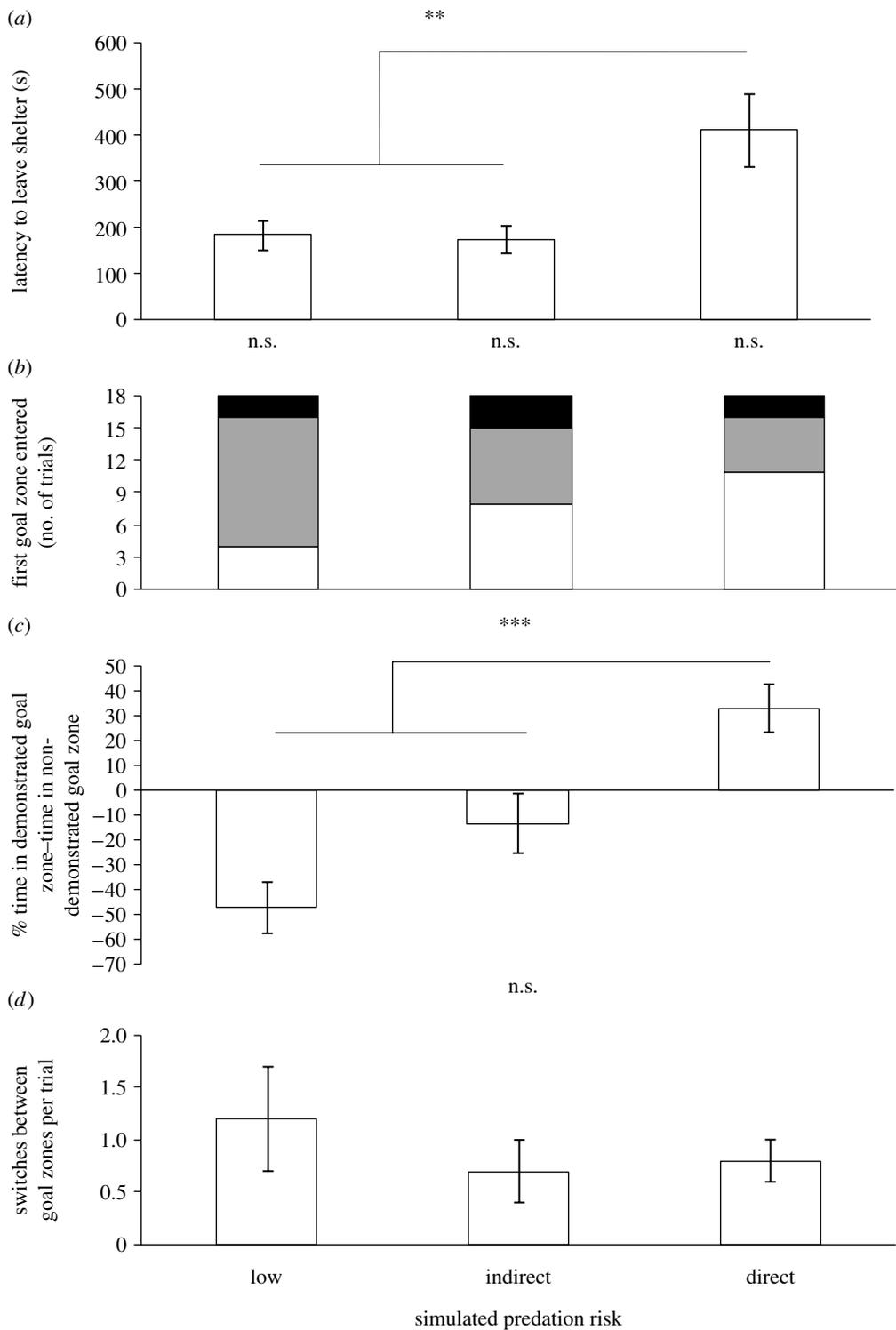


Figure 3. Experiment 2: social information versus existing private information. (a) The mean latency (\pm s.e.) of focal fish to emerge from the start box shelter. (b) The number of trials in which fish first entered the demonstrated (white) and non-demonstrated (grey) goal zones. Fish that failed to enter either are shown in black. (c) The mean difference between time spent in the demonstrated and non-demonstrated goal zones (\pm s.e.). A positive score indicates more time spent in the demonstrated goal zone, while a negative score indicates more time spent in the non-demonstrated goal zone. (d) The mean number of switches (\pm s.e.) made between goal zones by the focal fish. 'n.s.', no statistically significant difference.

goal quadrant than the non-demonstrated goal quadrant first (low risk: four entered the demonstrated goal quadrant first, 12 the non-demonstrated and two entered neither, $p=0.11$; indirect risk: eight entered the demonstrated goal quadrant first, seven the non-demonstrated and three entered neither, $p=1.0$; and high risk: 11 fish entered the demonstrated goal, five the non-demonstrated quadrant and two entered neither, $p=0.14$; figure 3b).

However, the difference in time spent in the two goal quadrants (samples recorded in the demonstrated goal quadrant (those in the non-demonstrated quadrant) was significantly greater in the high-risk treatment compared with the low- and indirect-risk treatments (ANOVA: $F_{2,53}=14.04$, $p<0.001$; Tukey's HSD *post hoc* analyses: $p<0.001$ and 0.01 , respectively). We also observed a difference between the low- and indirect-risk treatments

that approached significance (Tukey's HSD *post hoc* analyses: $p=0.07$; figure 3c).

Fish in the low-risk treatment group spent more time in the non-demonstrated goal zone, from which they had private experience of feeding, than they did in the demonstrated goal zone (Wilcoxon signed-rank test: $n=18$, $Z=-3.22$, $p=0.001$). Fish in the indirect-risk treatment group showed no preference for either goal zone ($n=18$, $Z=-1.06$, $p=0.288$), while those in the high-risk treatment group spent more time in the demonstrated goal zone than they did in the non-demonstrated goal zone ($n=18$, $Z=-2.87$, $p=0.04$).

We saw no difference between the three treatments in the total time spent in both goal quadrants combined (ANOVA: $F_{2,53}=0.73$, $p=0.48$), or in switching rates (ANOVA: $F_{2,53}=0.61$, $p=0.54$; figure 3d).

5. DISCUSSION

These experiments provide clear evidence that minnows increasingly rely on social learning as the basis for their foraging decisions as the perceived threat of predation risk increases. In accordance with our predictions, focal fish in both experiments spent more time in the demonstrated goal zone when under conditions of simulated predation risk than did fish in groups where risk was indirect or low. Under conditions of low risk, fish in experiment 1 showed no preference for either goal zone, and switched between zones frequently. By contrast, in the low-predation risk treatment in experiment 2, we saw that focal fish spent more time in the non-demonstrated goal zone, about which they had pre-existing private information, and showed no tendency to switch frequently between goal zones. These behaviour patterns are consistent with information gathering strategies based upon direct sampling and personal experience, respectively, but not social learning. Conversely, in both experiments we saw that focal fish in the high-risk condition, exposed to model predators, were strongly influenced in their patch choice by the apparent choices of conspecifics. These fish took longer to emerge from the start box than fish in other conditions, confirming that the presence of the model predators was sufficient to induce risk-averse behaviour in the focal fish. As anticipated, fish in the indirect-risk condition exhibited behaviour intermediate to those in the low- and high-risk conditions, with no clear patch preferences and only a weak and non-significant tendency to enter the demonstrated goal zone first in experiment 1. When perceived predation risk is equated to costly reliance on personal information, we can see that the findings are strikingly in accordance with the predictions for the usefulness of a 'copy-when-asocial-learning-is costly' strategy, and strongly imply that minnows exploit this social learning strategy. In contrast to Galef & Whiskin's (2006) experiment, in which they tested the same hypothesis, our patches were spatially segregated, allowing individual subjects potentially to attribute different estimates of risk to foraging at the two patches.

Our pilot experiment confirms that the observed feeder preferences are a consequence of focal fish using social information about patch quality to a greater extent under conditions of greater perceived risk, rather than an artefact of them simply moving to the last known location of the demonstrator group in order to gain shoaling benefits.

Focal fish in the pilot experiment showed no preference for the quadrant that had previously housed a group of conspecifics over one that had not, when no feeders were present. Our interpretation is also supported by the absence of a difference between conditions in the total amount of time spent in the two goal zones, for both experiments 1 and 2. Had the fish's decisions been solely based on the need to avoid predation, they should have spent decreasing amounts of time in the goal zones as the risk increased.

The idea that individuals should increase the extent to which they use social information when the costs associated with gathering new or using pre-existing private information become too great is an intuitive one. Despite this, previous evidence from empirical studies that have investigated the role of risk in mediating the use of social information by animals is equivocal. A study by Kendal *et al.* (2004) revealed that guppies (*Poecilia reticulata*) tended to use private information only when selecting where to feed when they were able to maintain visual contact with their shoal mates. If using private information meant losing contact with the shoal and forfeiting the anti-predator benefits of foraging as a group however, individuals preferentially fed at the same prey patch as the rest of the group, the least risky of the two options.

Eavesdropping by third parties during aggressive interactions might also constitute a strategy evolved to overcome the costs of private sampling (McGregor 1993). Here, private sampling would entail engaging in potentially costly fights with all competitors, whereas eavesdropping in this context is a social learning strategy that allows the observer to gauge the relative competitive abilities of others by monitoring their performance as they fight each other. Such a strategy allows individuals to minimize the potential costs when they come to fight themselves, either by rapidly escalating confrontations with known poor competitors, or by yielding to better ones.

Conversely, studies by Briggs *et al.* (1996) and Galef & Whiskin (2006) did not report enhanced use of social information under conditions where private sampling was costly. Briggs *et al.* (1996) failed to detect any influence of predation risk upon the incidence of mate choice copying by female guppies. They found that females preferred males that they had previously seen mating when predators were both present and absent. One potential explanation for this finding is that the benefits of mate choice copying always exceed those of privately inspecting potential mates and are independent of predation risk. Another is the fact that the guppies originated from a high-predation population, and that selection might therefore favour the adoption of behavioural strategies that always assume that predation risk is high. It is also possible that females become less choosy in the presence of predators, perhaps because both private sampling and social learning are more time consuming than randomly selecting between mates, with the latter strategy reducing exposure time to predators and therefore predation risk (Briggs *et al.* 1996).

Accordingly, our findings provide the first experimental confirmation, outside of humans, of formal theory that predicts that individuals should increase the extent to which they weigh and use socially acquired information when the potential costs of gathering or using private information are high (e.g. Boyd & Richerson 1985, 1988;

Feldman *et al.* 1996). Other models also predict that when the costs of sampling become too great, individuals should reduce assessment time accordingly (Giraldeau & Caraco 2000). Sampling costs might include time and energy invested in gathering information, or exposure to predation risk while doing so. For example, two models of mate choice behaviour predicted that both reducing available assessment time (Real 1990) and increasing predation risk (Crowley *et al.* 1991) act to decrease individual choosiness. Could these costs also exert influence upon choosiness when individuals must select not between pertinent cues from potential mates, but conflicting sources of private and social information? The findings of Briggs *et al.* (1996) and Galef & Whiskin (2006) are consistent with such an idea.

To the uninitiated, it may appear startling that the first confirmation of the costly information hypothesis, a theory proposed with humans in mind (Boyd & Richerson 1985), should come in a species of fish. However, social learning is now known to be widespread in fishes (Brown & Laland 2003), and, more generally, it is clear that the cognitive abilities of fishes have been largely underestimated (Brown *et al.* 2006). For instance, nine-spined sticklebacks have been shown to exhibit public information use, widely regarded as a cognitively challenging form of social learning (Coolen *et al.* 2003). The findings of this study imply that the evolved rules underlying the use of social learning by animals may apply across surprisingly broad taxonomic domains.

All the procedures were developed in full consultation with the local Home Office inspector, who judged that project licensing was not required. Fish had access to refuge (the start box) at all times during the trial. The short testing time (10 min post-emergence from the start box) ensured that exposure to the predator stimulus was brief. No fish suffered from health problems as a result of participating in the experiment.

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