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ORIGINAL ARTICLE

Michael M. Webster · Paul J. B. Hart

Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity

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Abstract Any mechanism that allows animals to increase their foraging efficiency is likely to be selected for, including the ability to learn to recognise and subsequently discriminate between habitat types based on their profitability. In a series of laboratory studies, we manipulated prey densities across two different experimental subhabitats and demonstrated that threespine stickleback (*Gasterosteus aculeatus*) can develop foraging preferences for subhabitats that have previously yielded prey. Fish were not recalling the spatial location of prey patches; rather, they were discriminating between subhabitats based on foraging experience there and allocating foraging effort accordingly. Foraging preferences took around 14 days to develop, and once established, they persisted independently of experimental prey density, suggesting that fish were using experience rather than real-time sampling to select foraging grounds. When we presented focal fish with social information cues, we found that they preferentially used local enhancement and current public information cues when they conflicted with previous experience, but that they did not use prior public information. This suggests that in the presence of conspecifics, individuals prioritise social conformity over the use of private information. We discuss our results in the context of optimal foraging and the trade-offs associated with balancing conflicting private and social information.

Keywords Optimal foraging · Social conformity · Public information · Memory · Threespine stickleback

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M. M. Webster (✉) · P. J. B. Hart
Department of Biology, University of Leicester,
Leicester, LE1 7RH, UK
e-mail: mmw5@le.ac.uk
Tel.: +44-116-2523350

Introduction

Fine-scale habitat structure can be unstable and subject to rearrangement through space and time, affecting the ability of foraging predators to detect prey. To optimise prey capture rates under such conditions and under the added constraints of competition from conspecifics and the risk of predation, the generalist forager would benefit from a flexible repertoire of behaviours allowing it to assimilate and process information from multiple sources. Such an individual potentially has the option of basing its foraging decisions upon private information, such as learned responses and prior experience arising from asocial interactions with the environment, or social information, i.e. cues generated by other foragers pertaining to the location, means of access to, or quality of a prey resource.

The process of discrimination between private and social information by animals is the subject of much ongoing research (Valone and Templeton 2002; Laland 2004). The common consensus is that private information is of greater value because it is more reliable and prevents the formation of informational cascades, whereby erroneous information is received and accrued, and suboptimal behavioural responses are elicited (Giraldeau et al. 2002; Kendal et al. 2006). Private information incurs a greater cost to the forager, however, since information must be gathered first hand. For this reason, and also because privately informed foragers faced with overwhelming contrary social information may be unwilling to make a unilateral decision which may trade away the benefits of social membership, the use of social information is reasoned to be likely widespread in nature (Danchin et al. 2004; Dall et al. 2005).

Shoaling fish represent ideal model systems for studying individual and social foraging behaviour since they are readily amenable to experimental manipulation in the laboratory. Previous studies have determined that various fish species are capable of assimilating and recalling private information concerning spatial and temporal cues to aid orientation and prey patch location (Milinski 1994; Odling-Smee and Braithwaite 2003). The capacity to recall and make use of such cues varies within and between species as a function of ecological conditions, in particular the temporal stability of the habitat (Mackney and Hughes 1995; Girvan and Braithwaite 1998; Hughes and Blight 1999), suggesting that the mechanism of recollection and utilisation of previous experience in fish is plastic and adaptive.

In nature, however, animals can select not only between patches of known spatial location but also between areas of unexplored subhabitat, structurally differing components of the greater forage plain. Examples of subhabitats in aquatic habitats may include deposits of different substrate materials, areas of different flow velocity and patches of different vegetation type. Differing subhabitats are known to harbour different assemblages of prey species (Taniguchi et al. 2003; Boyero and Bosch 2004; Taniguchi and Tokeshi 2004), facilitating the patchy distribution of prey assumed by many models of optimal foraging (Charnov 1976; Stephens and Krebs 1986). Through the discrimination of different subhabitat types, a predatory fish should be able to assess the potential of previously unsearched areas of subhabitat, providing that it has previously sampled an area of similar type and is able to recall its foraging success there. Evidence from field and laboratory studies has identified subhabitat preferences in species such as silver hake (*Merluccius bilinearis*; Auster et al. 1997, 2003) and threespine stickleback (*Gasterosteus aculeatus*; Webster and Hart 2004) that may be experience-based strategies, serving to actively enhance encounter rates with prey.

In addition to privately acquired information, shoaling fish also base foraging decisions on information obtained through the observation of the feeding performances of others (Laland and Williams 1997; Lachlan et al. 1998; Coolen et al. 2003; Kendal et al. 2004; van Bergen et al. 2004; Coolen et al. 2005). Such information may include local enhancement cues, which specifically relate to prey patch location, or public information cues, which infer prey patch quality (Coolen et al. 2003). Such cues may be current, in that they are available as the recipient is actively discriminating between patches, or they may be prior, in that they are provided before, but not during, the period when the recipient selects a foraging site. Given this, a forager may, therefore, potentially have several conflicting sources of information on which to base foraging decisions.

Using the threespine stickleback, we aimed firstly to determine whether individual fish were capable of developing foraging preferences for subhabitats based on their previous foraging successes there. Our second aim was to determine the strengths of these preferences when prey distributions between subhabitats did not correspond to those previously experienced. Finally, we looked at the use of previous experience by individuals in a series of trials in which focal fish were presented with a variety of different conflicting social information cues.

Materials and methods

Collection and housing of experimental fish

Approximately 500 subadult threespine stickleback measuring 15–20 mm total length were collected using dip nets in September 2004 from Stonton Brook, Leicestershire, UK. They were distributed between 12 holding tanks (40 × 25 × 28 cm deep, water depth 25 cm, bare Perspex substrate, water temperature 11°C, photoperiod 12:12 h) and fed daily to satiation on frozen Chironomid larvae. They were held under these conditions for approximately 4 months prior to the beginning of the study.

Subhabitat conditioning procedure

Fish were conditioned to display subhabitat foraging preferences prior to experimental trials. Conditioning was carried out in visually and chemically isolated tanks (40 × 25 × 28 cm deep, water depth 25 cm), each of which was divided into two equally sized sections of two types of substrate material over which fish foraged for benthic prey items. One substrate comprised fine sand (grain size≤1 mm) and the other comprised assorted angular sandstone gravels, where particles had a longest axis length range of 5–20 mm. These two substrate types represented different subhabitat units, similar to those that river-dwelling fish may encounter in nature. Each tank held four fish, size-matched to one another to within <1 mm total length. Over the course of a conditioning period prey, 5-mm sections of thawed Chironomid larvae were provided in one subhabitat only. These were provided in excess once per day and were distributed evenly across the surface of the subhabitat using a 1-cm^3 syringe. The duration of the conditioning period and the subhabitat to which fish were conditioned varied between experiments, as described below.

Experimental tank and procedure

Subhabitat preference binary choice trials were conducted in an experimental tank (54 × 25 × 30 cm deep, water depth 25 cm), covered at the sides with opaque plastic to eliminate outside disturbance. The tank contained two subhabitat types of equal area, containing the same substrate materials that the fish had experienced during the conditioning phase of the experiments. The left–right positioning of these substrate materials within the tank was randomised for each trial to eliminate any tank end bias. Prey items were randomly distributed across each subhabitat; prey densities varied between experiments as stipulated in the experimental descriptions below. Sections of Chironomid larvae 5 mm in length were used as prey in all trials.

Fish were deprived of food for 18 h prior to testing to increase foraging motivation. Before the start of each trial, the test fish was held for 3 min in a 25-cm-tall mesh holding tower (mesh size 2 mm) in the centre of the binary choice tank, such that it could view both substrate types. The tower was raised and removed, releasing the fish to explore the tank, and the trial began when the fish located and consumed the first prey item. With this approach, we could be certain that the fish has made the transition from any stress-related behaviour to the foraging behaviour that we were seeking to quantify. Each trial lasted 3 min, and we recorded the amount of time spent directly over, but less than 10 cm above each substrate, and the number of feeding strikes made into each subhabitat type. Multiple consecutive strikes made at a single prey item were deemed to constitute a single handling process and were recorded as such.

Control experiment: pre-existing subhabitat preferences

A previous study revealed pre-existing subhabitat preferences in threespine stickleback (Webster and Hart 2004). We reasoned that any pre-existing preferences should not persist over the 4-month period during which fish were held in the laboratory prior to the beginning of the experimental series. To confirm this assumption, we conducted a control experiment in which fish that had not experienced either substrate type were given a binary choice using the tank and protocol described above. One randomly selected fish per holding tank (*n*=12) was tested for subhabitat preference at an experimental prey density ratio of 1:1 (0.008 prey item/cm^2 on each substrate type).

Experiment 1: the rise of subhabitat foraging preferences

The purpose of this experiment was to determine whether subhabitat foraging preferences arose in response to experience of successful foraging on a given subhabitat type. Twenty-four groups of four fish were established in their own subhabitat conditioning tanks as described above. Initially, we provided prey on the sand subhabitat only. Every second day for 32 days, one fish was randomly selected from each group and tested for subhabitat preference using the procedure and binary choice tank described above. After 18 days, we randomly selected 12 of the 24 groups and switched prey provision from the sand to the gravel subhabitat type. Binary choice testing continued as previously; this allowed us to observe the rate at which a preference arose for the sand subhabitat containing prey and at what rate it decayed and was replaced when only the gravel subhabitat held prey. In the remaining 12 groups, we continued to provide prey on the sand subhabitat only; these groups served as controls, for comparison with those groups in which prey provision was switched. Preferences were examined at only one experimental prey density ratio, 1:1 (0.008 item/cm^2 in each subhabitat in the experimental tank).

Experiment 2: recent experience vs conflicting real-time assessment

In this experiment, we aimed to determine whether test fish that had experienced predictable and regular prey distribution over the course of a conditioning phase would use previous experience alone to select between subhabitats or whether they would use what we termed real-time assessment. By the definition used in this study, real-time assessment would involve visiting both subhabitat types and allocating proportionally more foraging effort to that which held more prey, following the assumptions of the ideal free distribution (Milinski and Parker 1991; Fretwell and Lucas 1970). We achieved this by presenting test fish with binary choice tests in which prey density between subhabitats varied from what they had previously experienced, such that using previous experience alone would not provide optimal foraging returns.

Twenty-four groups of four fish were established in their own subhabitat conditioning tanks as described above. In the first 12 of these tanks, prey was provided on only the sand subhabitat, and in the second 12, only on the gravel subhabitat. Fish were held under these conditions for a period of 14 days.

Following this conditioning period, we tested subhabitat preferences of fish conditioned on the sand and gravel subhabitat under four different prey density ratios: (1) 1:1, sand/gravel (0.008 item/cm^2 in each subhabitat); (2) 3:1 (0.024 item/cm^2 in the sand vs 0.008 item/cm^2 in the gravel subhabitat); (3) 1:3 (0.008 item/cm^2 on the sand vs 0.024 item/cm^2 in the gravel subhabitat); (4) 0:0, a control with no prey present in either subhabitat. Trials were conducted using the experimental tank and procedure described above. One fish from each conditioning tank was tested at each prey density ratio, giving 12 trials per treatment, and over the course of the experiment, no fish was tested more than once.

Experiment 3: recent experience vs conflicting local enhancement and public information

In this experiment, we aimed to determine whether test fish persisted in the use of recent experience when contradictory local enhancement and current and prior public information cues were available from stimulus conspecifics.

Thirty-six groups of four fish were established in their own subhabitat conditioning tanks as described above. Twelve groups were used for each of three parts of experiment 3. In all groups, fish were conditioned to preferentially forage on the sand substrate type for 14 days prior to testing. Additionally, we set up 12 identically sized tanks of four fish each in which the substrate was bare Perspex. These were size-matched to the experimental fish, but had had no experience of either substrate type during the 6-month period for which they had been held in the laboratory. These were also held for 14 days.

Local enhancement

To the experimental test tank, as described above, we added two stimulus chambers, 25 cm tall, 10 cm diameter clear acrylic cylinders with four 2-mm diameter perforations per centimeter squared of vertical surface and a clear unperforated acrylic base covered with the corresponding substrate material. Each chamber was placed centrally within one of subhabitat types and contained a group of stimulus fish, size-matched to one another and to the focal fish. These were randomly drawn from laboratory stock tanks housing fish that were not otherwise used in this study. Test fish had had no prior experience of these fish and therefore were unfamiliar with them. No stimulus fish was used more than once.

We conducted four sets of trials: eight fish in the sand subhabitat vs three in the gravel subhabitat, suggesting better foraging in the sand subhabitat (Coolen et al. 2005), and in agreement with previous experience; three fish in the sand subhabitat vs eight in the gravel subhabitat, in contradiction to previous experience; and two control experiments. In the first control, three fish were present in each subhabitat, and the focal fish was conditioned to prefer the sand subhabitat as in the previous two trial sets. In the second control, three fish were also present in each subhabitat; however, the focal fish were derived from the Perspex substrate tanks and had no pre-existing subhabitat preference. Test fish were held in the holding tower as described in the experimental tank procedure above for 3 min, during which time they could observe both stimulus shoals. Prey density was equal on both substrate types outside the stimulus chambers, with 0.008 prey item/cm^2; no prey was provided within the stimulus chambers. Trials progressed and data were collected as described above.

Current public information

The experimental test tank was set up with the stimulus chambers as described above for the local enhancement trials. In this set of trials, prey was provided within the stimulus chambers as well as outside, allowing the stimulus fish to feed and the focal fish to monitor them. Prey items were introduced into the bottom of each stimulus chamber from a syringe, via a 10-mm diameter opaque acrylic tube after the 3-minute settling period of the focal fish and immediately before it was released. The acrylic tube prevented the focal fish from seeing the delivery of the prey into the stimulus chamber. The substrate within the stimulus chamber was set lower than the surrounding substrate so that the focal fish was unable to see the prey within the chamber after its delivery. We conducted four sets of trials. Stimulus shoals each comprised three size-matched fish on either substrate in each trial set. In the first trial set, the stimulus chamber in the sand subhabitat was provided with 30 prey items, compared to 10 in the stimulus chamber in the gravel subhabitat, suggesting better foraging in the sand subhabitat, in agreement with previous experience. In the second trial set, the number of prey items delivered to each stimulus chamber was reversed, suggesting better foraging in the gravel subhabitat, in contradiction to previous experience. In the third trial series, 10 prey items were delivered to each stimulus chamber. In the final trial series, 10 prey items were also provided to each; however, the focal fish were derived from the Perspex substrate tanks and had no pre-existing subhabitat preference. Stimulus fish readily consumed prey items in all trials, though in no trial were all prey items within a stimulus chamber seen to be consumed before the trial ended. Prey density was equal on both substrate types outside the stimulus chambers, with 0.008 prey item/cm^2.

Prior public information

The procedure for assessing the influence of prior public information upon the foraging decisions of the focal fish was identical to that used in the current public information trial series, with the exception that the foraging cues provided by the stimulus fish were provided before the focal fish was allowed to forage. The focal fish was held in the holding tower for a 3-min period as previously. This was followed by the introduction of prey items to the stimulus chambers, also as previously. The focal fish, still within the holding tower, was allowed to observe the stimulus shoals feeding for 3 min, after which the stimulus shoals were removed. The focal fish was given a further 1-min settling period and was then released from the holding tower, allowing the trial to progress as described above. There were four trial sets as described in the current public information section, and the prey density was equal on both substrate types outside the stimulus chambers, with 0.008 prey item/cm^2, also as above.

Statistical analysis

In part 1, for within-treatment analyses, both time allocation and foraging rate data were analysed using Friedman tests, a non-parametric repeated measures test. For post hoc analyses, we used equal groups paired comparisons as described by Langley (1979, p 220). To make comparisons between treatments, we used Wilcoxon signed rank tests.

In the control experiment, and in parts 2 and 3, we analysed time allocation and foraging rate data as follows: the proportion of time allocated to each subhabitat was converted to a proportion of the total trial time, and the proportion of time allocated to the gravel subhabitat was then subtracted from that allocated to the sand subhabitat. These difference values were compared with a null expected value of zero using one-sample *t* tests. Foraging rates were compared using Wilcoxon signed rank tests.

Results

Control experiment: pre-existing subhabitat preferences

The amount of foraging effort directed by fish to either experimental subhabitat was not statistically different, either in terms of time allocation (one-sample *t* test: $t_{(11)}$=0.76, *P*=0.46), or foraging rate (Wilcoxon signed ranks test: *n*=1, 11 *Z*=−0.70 *P*=0.48).

Experiment 1: the rise of subhabitat foraging preferences

The pattern of proportional time allocation to the subhabitats in the experimental treatment was seen to vary significantly over the duration of the study (Friedman test: $X^2_{(1,15)} = 137.90$, *P*<0.001). Post hoc analysis revealed that the allocation of time to the sand subhabitat became significantly different from the first day of testing on day 14 (*P*=0.05). Prey provision was switched to the gravel subhabitat on day 18; a post hoc test showed that fish were allocating significantly more time to this subhabitat compared to day 18 by day 24 (*P*=0.01).

The proportional time allocation of the control treatment, in which prey provision was not switched, also varied significantly over the course of the study (Friedman test: $X^2_{(1,15)} = 137.90$, *P*<0.001). A significant preference for the sand subhabitat arose by day 16 (Post hoc analysis: *P*=0.01), but there was no subsequent significant switch in subhabitat preferences as seen in the experimental treatment (Fig. 1).

As such when the patterns of time allocation were compared between the experimental and control treatment groups, they were found to differ significantly (Wilcoxon signed ranks test: *Z*=−15.98, *n*=16, *P*<0.001).

This pattern was also seen in the direction of foraging effort over time in the experimental treatment (Friedman test: $X^2_{(1,15)} = 75.37$, *P*=0.001). In this treatment, foraging effort allocation to the sand subhabitat increased form the beginning of the study, becoming significantly different from the first day of testing by day 14 (Post hoc analysis: *P*=0.05). Following the switching of prey provision to the gravel subhabitat, fish began allocating more foraging effort there, showing a significant preference for that subhabitat by day 26 compared to day 18 (Post hoc analysis: *P*=0.001).

In the control treatment, there was an initial increase over time in the allocation of foraging effort to the sand subhabitat ($X^2_{(1,15)} = 26.19$, *P*=0.03), which became significantly different from that seen on the first day of testing by day 16 (Post hoc analysis: *P*=0.05). As with time allocation, there was no subsequent switch in subhabitat preference in the control treatment (Fig. 1).

The pattern of forage rate allocation was significantly different between treatments (Wilcoxon signed ranks test: *Z*=−15.67, *n*=16, *P*<0.001).

Experiment 2: recent experience vs conflicting real-time assessment

Test fish provided with previous experience of finding prey in either gravel or sand subhabitats displayed significant foraging preferences for that subhabitat in trials. This

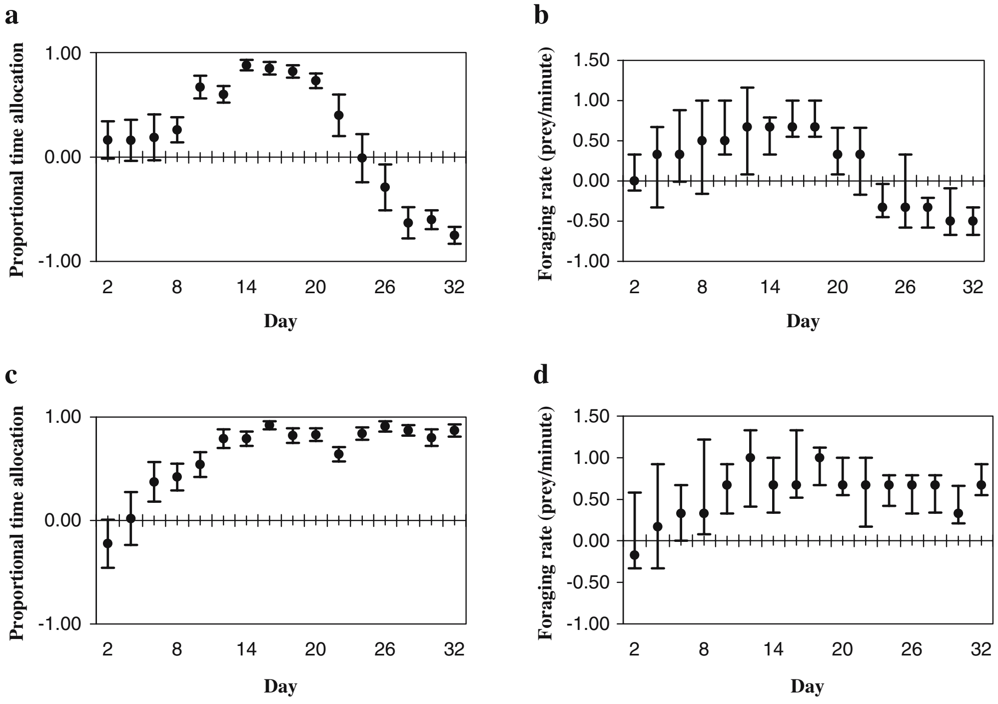

Fig. 1 **a** Changes over the course of the experiment in the proportional time allocation (mean±standard error). **b** The foraging rate (prey strikes per minute±quartiles) of fish to either subhabitat type in trials where prey was provided in the sand subhabitat only up until day 18 of the study and was switched to the gravel subhabitat thereafter. **c**, **d** Time allocation and foraging rates over time in control trials in which prey was provided only on the sand subhabitat for the duration of the study. In all graphs, a positive value indicates preference for the sand subhabitat, and a negative value indicates preference for the gravel subhabitat

was reflected both in the allocation of time and foraging rate (Fig. 2).

Prey provided on the gravel subhabitat

Similarly, time allocation to the gravel subhabitat was also significantly greater in trials where prey density was equal and where it was greater in either the gravel or the sand subhabitat (one-sample t test: $t_{(11)}=-2.99$, $P=0.01$; $t_{(11)}=-2.44$, $P=0.03$; and $t_{(11)}=-2.99$, $P=0.01$, respectively). As previously, this preference was also reflected in the foraging rates (Wilcoxon signed rank test: $Z=-2.50$, $n=12$, $P=0.01$; $Z=-2.74$, $n=12$, $P=0.006$; and $Z=-2.25$, $n=12$, $P=0.02$, respectively). Also as previously, in trials where no prey was present, no time allocation preferences were seen ($t_{(11)}=-1.14$, $P=0.27$; Fig. 2a,b).

Prey provided on the sand subhabitat

Time allocation to the sand subhabitat was seen to be significantly greater when prey density was equal in both subhabitats, when it was greater in the sand subhabitat, and even when it was greater in the gravel subhabitat (one-sample t test: $t_{(11)}=3.03$, $P=0.01$; $t_{(11)}=5.48$, $P<0.001$; and $t_{(11)}=2.55$, $P=0.02$, respectively). This was also true of the foraging rate (Wilcoxon signed rank test: $Z=-2.56$, $n=12$, $P=0.009$; $Z=-2.93$, $n=12$, $P=0.007$; and $Z=-2.28$, $n=12$, $P=0.01$, respectively). However, in trials where no prey was present in either subhabitat, no time allocation preferences were seen ($t_{(11)}=-0.12$, $P=0.89$; Fig. 2c,d).

Experiment 3: recent experience vs conflicting local enhancement and public information

Local enhancement

Fish were seen to display time allocation preferences and greater foraging rates in the sand subhabitat when it held the larger stimulus shoal (time allocation, one-sample t test: $t_{(11)}=11.74$, $P<0.001$; foraging rate, Wilcoxon signed rank test: $Z=-3.02$, $n=12$, $P=0.002$). When the stimulus shoal was larger on the gravel subhabitat, they displayed a greater time allocation, but no difference in foraging rate (one-sample t test: $t_{(11)}=-6.32$, $P<0.001$; Wilcoxon signed rank test: $Z=-1.16$, $n=12$, $P=0.10$). In trials where the stimulus shoals were identical in size, no preference for either subhabitat was seen, either where test fish had been conditioned to prefer sand subhabitat (one-sample t test: $t_{(11)}=0.75$, $P=0.46$; Wilcoxon signed rank test: $Z=-0.05$, $n=12$, $P=0.95$) or where they had no previous experience of either (one-sample t test: $t_{(11)}=-0.81$, $P=0.43$; Wilcoxon signed rank test: $Z=-0.36$, $n=12$, $P=0.75$; Fig. 3a,b).

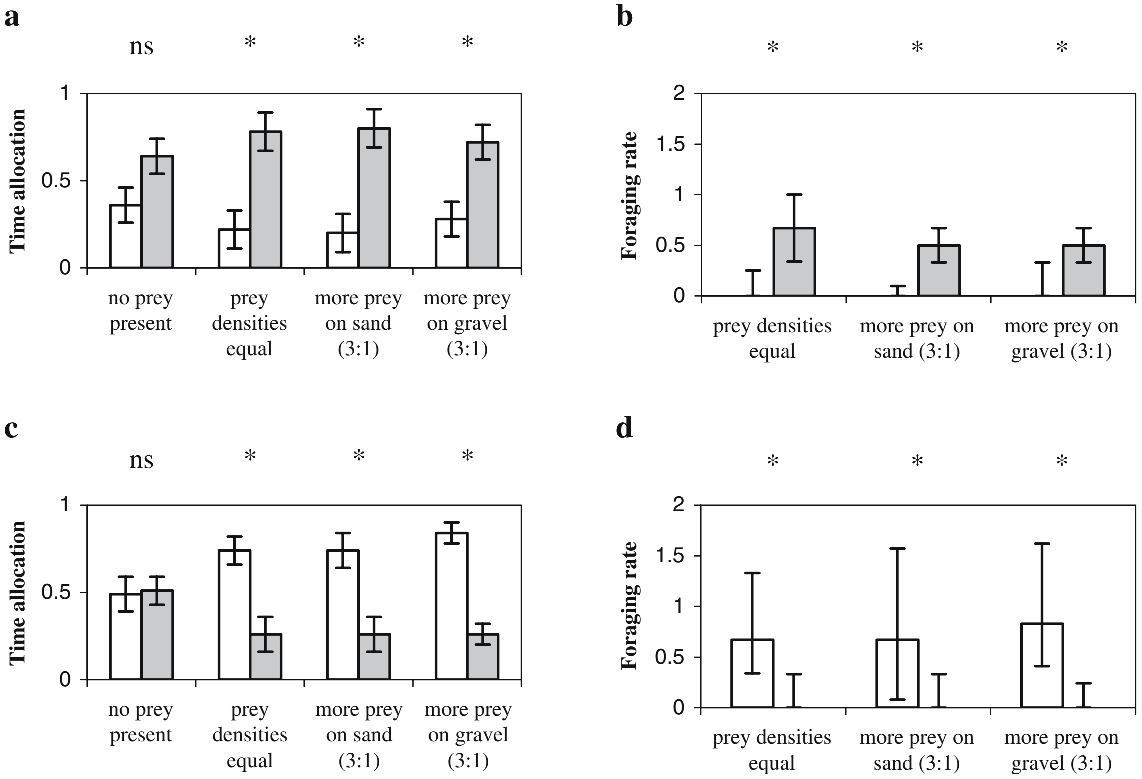

Fig. 2 **a** The proportional time allocation (mean±standard error). **b** The foraging rate (prey strikes per minute±quartiles) of fish conditioned to preferentially forage in the gravel subhabitat. **c** The proportional time allocation. **d** The foraging rate of fish preconditioned to preferentially forage in the sand subhabitat. *Grey bars* represent the gravel, and *white bars*, the sand subhabitats, respectively. *$P<0.05$. *ns* Non-significant

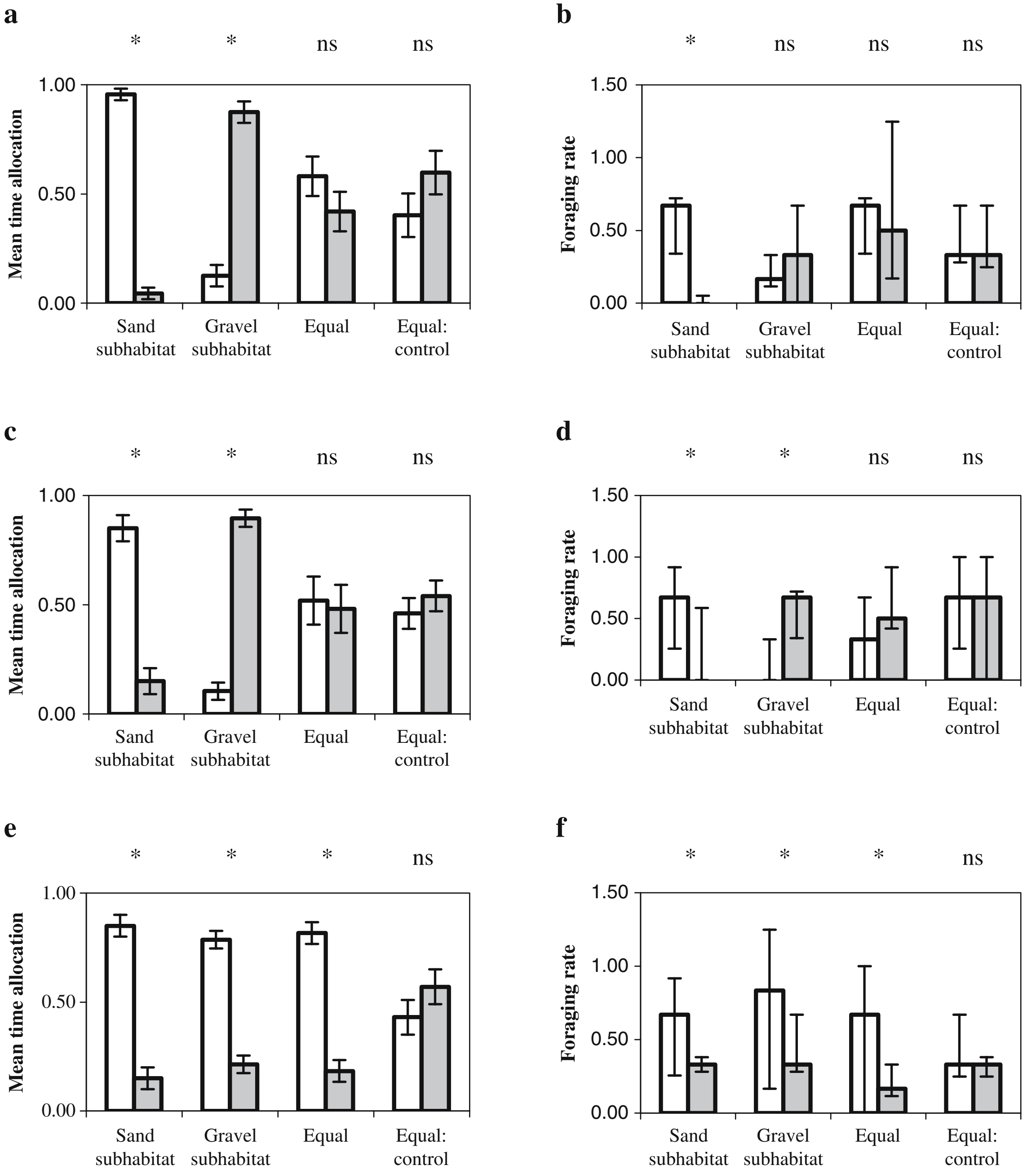

Fig. 3 Fish were conditioned to preferentially forage in the sand subhabitat. **a**, **b** The proportional time allocation (mean±standard error) and the foraging rate (prey strikes per minute±quartiles), respectively, when local enhancement cues were provided. **c**, **d** Proportional time allocation and the foraging rates when current public information cues were provided. **e**, **f** Proportional time allocation and the foraging rates when prior public information cues were provided. *X-axis labels* indicate the subhabitat of inferred higher quality, and control refers to trials in which test fish had no preconditioned subhabitat preference. *Grey bars* represent the gravel, and *white bars*, the sand subhabitats, respectively. *$P<0.05$. *ns* Non-significant

Current public information

When current public information cues were available, test fish were seen to direct greater time allocation and foraging rate to the subhabitat indicated to be of higher quality. This was true when greater quality was inferred both of the sand subhabitat (one-sample *t* test: $t_{(11)}=5.34$, $P<0.001$; Wilcoxon signed rank test: $Z=-2.03$, $n=12$, $P=0.02$) and the gravel subhabitat (one-sample *t* test: $t_{(11)}=-7.29$, $P<0.001$; Wilcoxon signed rank test: $Z=-2.69$, $n=12$, $P=0.007$). However, when both subhabitats were indicated to be of equal quality, no preference existed (one-sample *t* test: $t_{(11)}=0.30$, $P=0.76$; Wilcoxon signed rank test: $Z=-0.25$, $n=12$, $P=0.79$). Likewise, no preference existed in fish that had no previous experience of either subhabitat when both subhabitats were indicated to be of equal quality (one-sample *t* test: $t_{(11)}=-0.55$, $P=0.59$; Wilcoxon signed rank test: $Z=-0.17$, $n=12$, $P=0.86$; Fig. 3c,d).

Prior public information

Test fish apparently made no use of prior public information, eliciting a preference for the sand subhabitat to which they were preconditioned in trials where the sand subhabitat was previously indicated to be of higher quality (one-sample t test: $t_{(11)}=5.66$, $P<0.001$; Wilcoxon signed rank test: $Z=-2.53$, $n=12$, $P=0.01$), where the gravel subhabitat was previously indicated to be of higher quality (one-sample t test: $t_{(11)}=5.04$, $P<0.001$; Wilcoxon signed rank test: $Z=-2.95$, $n=12$, $P=0.003$) and when both patches were indicated to be of equal quality (one-sample t test: $t_{(11)}=5.03$, $P<0.001$; Wilcoxon signed rank test: $Z=-2.84$, $n=12$, $P=0.004$). In trials where test fish had no previous experience of either subhabitat, when both subhabitats were previously indicated to be of equal quality, no preference was seen to exist (one-sample t test: $t_{(11)}=-0.99$, $P=0.34$; Wilcoxon signed rank test: $Z=-1.08$, $n=12$, $P=0.28$; Fig. 3e,f).

Discussion

Individual test fish acquired foraging preferences for subhabitats in which prey had previously been consistently presented. These arose gradually (experiment 1) and were maintained in experimental trials irrespective of the actual prey densities in either subhabitat (experiment 2). When local enhancement and current public information cues were provided, they were used by individuals in place of previous experience. Fish did not use prior public information, however, and individuals tested in the absence of stimulus shoals that they had just observed feeding reverted to foraging preferences consistent with their previous experience (experiment 3). A control experiment revealed that fish had no pre-existing foraging preferences for either experimental subhabitat type.

We showed that once established, preferences were strong, with fish selecting the subhabitat in which they had previous experience of finding prey irrespective of its actual prey density relative to the other subhabitat (experiment 2). Particle size differed between subhabitats, and this probably influenced the availability of visual and chemical cues pertaining to the location of prey items since the larger inter-particle voids in the gravel subhabitat could have obscured prey. Nevertheless, test fish conditioned to find prey in either subhabitat displayed foraging preferences there subsequently. Such a behavioural strategy appears to be maladaptive and is contrary to optimal foraging theory (Charnov 1976; Stephens and Krebs 1986), which predicts that foragers should sample patches frequently, amassing and updating accurate information on each. Interestingly, earlier studies reveal that other species, including walleye pollock (*Theragra chalcogramma*; Ryer and Olla 1995), Atlantic cod (*Gadus morhua*; Steingrund and Fernö 1997) and turbot (*Scophthalmus maximus*; Ellis et al. 2002) continue to exploit prey types or to persist in the use of foraging tactics that have recently yielded optimal returns, even when doing so becomes apparently suboptimal. It is possible that if prey yield is consistently predictable in a certain subhabitat, it may become less costly to forage there than to expend effort and incur risk in sampling areas that have held fewer prey on earlier occasions. In our study, following the change in the provision of prey to the gravel subhabitat (experiment 1), preference for the sand subhabitat was seen to persist initially before steadily degrading. This may be an example of reversal learning (Frank et al. 1972; Levin and Vergara 1987), generally considered to be costly since individuals must learn to recognise and handle new resources.

Additionally, we found that fish did not display any significant subhabitat preference when no prey was provided (experiment 2). These findings suggest that positive reinforcement through the presence of prey is required for subhabitat preferences to persist. This could serve to readjust foraging preferences, countering maladaptive behaviours in which fish persistently exploit habitat or prey types that no longer provide optimal returns. The rate at which individual foraging preferences arise and decay may be linked to the temporal stability of the habitat in which the fish lives, something that has previously been shown to affect spatial memory capacity and retention (Mackney and Hughes 1995; Warburton 2003).

Individuals made use of local enhancement and current public information cues irrespective of their previous experience, foraging in the subhabitat of inferred higher quality or partitioning effort equally between subhabitats when public information suggested no difference existed between them. We found that when local enhancement cues were provided, fish always preferred to forage in the subhabitat that held the largest shoal. This is contrary to the dictates of ideal free distribution theory, but similar to the findings of Gotceitas and Colgan (1991), who documented a similar preference for association with numerically larger groups, suggesting that foraging fish may use the numbers of conspecifics at prey patches as a proxy to infer patch quality. Social foraging facilitates greater prey detection rates (Pitcher et al. 1982; Pitcher and Magurran 1983; Lachlan et al. 1998; Day et al. 2001), and the potential returns from foraging as a group member in an unknown subhabitat may outweigh those from foraging as a singleton or in a smaller group, even in a previously preferred area. In addition to the numbers of foragers present, their feeding rates also provide information on patch quality (Coolen et al. 2003). If this information is available to an individual during the period in which it is selecting between patches, then it represents a more recent and reliable source than any private information coming from previous experience and should therefore be given more weighting. As in our study, Coolen et al. (2003) found that threespine stickleback did not however use prior public information. They went on to show that the closely related ninespine stickleback (*Pungitius pungitius*) did so, drawing upon cues from con- and heterospecifics alike. This interspecific difference is likely explained by the differences in habitat use and behaviour that separate and define their respective niches (Hart 2003). The ninespine stickleback has less robust bodily armour than that of the threespine stickleback, making it more vulnerable to predation, and it has been suggested that it therefore relies to a greater extent upon public information, which can be collected from cover (Coolen et al. 2003).

The adaptive benefits of using previous experience to enhance future foraging successes are clear since the use of recalled information relating habitat structure to prey yield allows the potential to forage in a non-random manner, even in unexplored areas. Nonetheless, we exercise caution when considering the utility and prevalence of these behaviours in nature. Our study provides strong evidence of the use of private information by individuals, but suggests that in the more naturally realistic situation of social foraging, public information use and social conformity predominate. We suggest that private information such as recent experience may be used by foragers in situations where public information is limited or lacking completely, where risks associated with social nonconformity, such as enhanced predation risk, are low, or where potential payoffs from unilateral decision making are high. This is consistent with the social release hypothesis (Brown and Laland 2002), which suggests that whilst social conformity prevails, in the absence of demonstrators, naïve individuals have the opportunity to innovate. To support these assertions, we require data from well-designed field-based studies.

The decision-making process employed when discriminating between private and public information is likely to be influenced by environmental factors, including predation pressure. The threespine stickleback used in our study originated from a channel in which predation risk is probably relatively high, given the presence of a number of piscivorous fish and bird species. Accordingly, it may be better to conform and shoal rather than to forage independently and risk predation, and this may also explain why fish in our local enhancement experiment opted to join the larger stimulus shoal. Previous studies have shown that species including ninespine stickleback (Coolen et al. 2005; van Bergen et al. 2004) and guppies (*Poecilia reticulata*; Kendal et al. 2004) discriminate between private and social information, selecting the most reliable source and foregoing social conformity only when the potential costs of doing so are low.

Guppies from sites where predation risk is less intense are known to form smaller, less cohesive shoals than those from sites of relatively high predation risk Magurran and Seghers 1990, 1994; Seghers and Magurran 1995). It is conceivable that in such sites, individuals may give more weighting to private information and personal experience when making foraging decisions. Furthermore, hungry fish may trade off the benefits of shoaling to improve their potential share of any prey that is found (Krause 1993). Internal state, a relative constant in our study, could therefore also be a factor in determining which information source is acted upon. More research in these areas would be valuable.

Related to this are implications for group decision making. Group composition can be highly ephemeral (Hoare et al. 2000), and threespine sticklebacks have been shown to discriminate between conspecifics with similar and differing recent habitat and prey use history from their own (Ward et al. 2004, 2005). Further work could therefore assess the importance of recent habitat and diet experience in shoal structuring and collective behaviour. There exists the possibility for information use and habitat selection to vary at both the individual and the group levels, and this has important implications for our broader understanding of sociobiology and ecology.

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