

Diet-specific chemical cues influence association preferences and prey patch use in a shoaling fish

M. M. WEBSTER, E. L. ADAMS & K. N. LALAND

School of Biology, University of St Andrews

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In many social species individuals have to make adaptive decisions about with whom to group. Self-referent matching of chemical social information specific to patterns of diet and habitat use is an important factor underlying social organization in shoaling fishes. In a series of three experiments, we gave female Whitecloud mountain minnows, *Tanichthys albonubes*, a binary choice between shoaling with stimulus groups fed upon the same or a different diet to themselves. Focal fish spent significantly more time shoaling with the group whose individuals had consumed the same diet as themselves, were significantly more likely to follow such a group when the two stimulus groups diverged in a simulated shoal fission event, and were significantly more likely to feed from a prey patch containing a neutral food that was situated close to the same diet stimulus group than from an identical one located close to the stimulus group fed the alternative diet. By grouping with others that are exploiting the same resources, individuals potentially gain useful information about the location of resources.

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Group living is a widespread phenomenon, providing individual group members with a range of benefits that they might otherwise forgo by living alone (Krause & Ruxton 2002). Social organization relies critically upon recognition of suitable groupmates. In many social aggregations the structure of the group can change through fission and fusion processes as new individuals arrive and larger groups split into fragments, a process driven by various passive and active mechanisms, and underpinned by a range of predation, foraging and reproductive selection pressures (Raman 1997; Hoare et al. 2000; Croft et al. 2003). If individuals are to maximize the benefits that they gain from living in groups, they may therefore have to make frequent decisions about which groups to join, and with which individuals to associate within those groups.

Shoaling fishes have proven to be a useful study system for empirical investigations of the mechanisms and trade-

offs underlying social organization in animal groups (Brown et al. 2006). Natural fish shoals tend to be highly sorted by a number of general factors including size, species, age class and other phenotypic characters (Krause et al. 1996; Hoare et al. 2000), as well as by more subtle criteria such as specific recognition and a preference for familiar individuals (Griffiths & Ward 2006). In some fishes, self-referent matching of resource-specific chemical cues directly affects shoaling preferences, with individuals preferentially grouping with others that have recently consumed the same types of prey or occupied the same microhabitats as themselves. This has been shown for diet cues in Arctic charr, *Salvelinus alpinus* (Olsen et al. 2003) and guppies, *Poecilia reticulata* (Morrell et al. 2007) and for both habitat and diet use in three-spined sticklebacks, *Gasterosteus aculeatus*, both in the laboratory (Ward et al. 2004, 2005; Webster et al. 2007, 2008) and in the wild (Ward et al. 2007).

Fish may accrue a number of benefits from joining shoals that are exploiting the same resources as themselves. Self-referent matching of prey cues might allow an

Correspondence: M. Webster, School of Biology, Bute Building, University of St Andrews, Fife KY16 9TS, U.K. (email: mmw1@st-andrews.ac.uk).

individual to gather social information from more knowledgeable shoalmates about the location and quality of specific prey resources within an area. Fish might also use habitat-specific olfactory cues generated by others as a means of navigating within their social environment, a strategy that might be especially useful to species with low shoal fidelity but high site fidelity (Ward et al. 2007; Webster et al. 2007).

In this study we sought to explore two further aspects of shoaling preferences based upon resource cue matching, looking first at whether individuals use self-referent matching to select between diverging groups during a simulated shoal fission event, and second at whether shoaling preferences based upon such cues affect individual prey patch selection. Previous studies of resource cue matching have considered only the shoaling preferences of fish that were choosing between stationary stimulus shoals. In nature, however, decisions must often be made while on the move, and shoaling choices must be made rapidly if the choosing individual is to avoid the costs of making suboptimal shoaling decisions or even becoming separated from the group. Given this, we predicted that focal Whitecloud mountain minnows, *Tanichthys albonubes* (Cyprinidae), would identify and join moving stimulus shoals that had consumed the same prey as themselves more often than they would follow stimulus fish that had consumed an alternative diet. We then went on to investigate the influence of such shoal choice decisions upon prey patch selection of focal fish. We predicted that fish would not only shoal with others that had consumed the same prey, but that they would also feed near them, even when otherwise identical patches of a neutral food were situated close to other stimulus fish that had fed on an alternative diet.

GENERAL METHODS

Subjects and Apparatus

Whitecloud mountain minnows are a small, shoal-forming freshwater fish, ecologically similar to the zebra fish, *Danio rerio*, and are an ideal study species for the experimental investigation of social organization. We obtained fish from a local supplier, Ultimate Aquatics, Cupar, Fife, U.K. In the laboratory they were housed in 30-litre housing tanks at a density of 25 fish per aquarium. The sides and rear of each tank were covered with opaque plastic sheeting to minimize disturbance from outside, and each contained a layer of 5 mm gravel, 3 cm deep, an air-powered filter and several artificial plants to provide cover. The water temperature was held at 20 ± 2 °C, and the light:dark regime at 12:12 h (lights on at 0700 hours) for the duration of the study. The fish were fed twice daily with standard flake fish food and 30% of the water was changed once per week. The fish were held under these conditions for several weeks before the experiments began. Only females measuring approximately 2.5 cm in length were used in the experiments described below. This species is sexually dimorphic and females were easily identified. To avoid courtship behaviour and related aggression, we did not use males or mixed sex groups.

Procedure

We carried out three experiments, adopting a protocol in which a focal fish was presented with a binary choice between shoaling with one of two stimulus groups that had been fed on either the same or a different diet as its own. We used two experimental foods, consisting of either frozen bloodworms or *Daphnia* (both from Tetra GmbH, Herrenteich 78, 49324 Melle, Germany), both of which were known to be unfamiliar to the fish.

We established a pool of approximately 100 stimulus fish, all of which were drawn from four of the housing tanks described above. These were then divided between 10 30-litre housing tanks (i.e. ca. 10 fish per tank), fitted with air-powered filters and artificial plants as described above, but with no gravel substrate. This pool of focal fish was used throughout the study. On any one day of testing we carried out 10 trials, using a total of 50 stimulus fish. In experiments 1 and 3 there were 3 days of testing each, giving a total of 30 replicates. In experiment 2 there were 5 days of testing; however, on the final day only eight trials were carried out, giving a total of 48 replicates. Trials were never conducted 2 days running, and stimulus fish were therefore never used on consecutive days. Stimulus fish were fed one experimental diet, either bloodworm or *Daphnia* only, throughout the study, and were always fed flake food on the days that they were not being used in trials. Before being tested, stimulus fish were first deprived of food for 24 h to standardize hunger levels and to ensure that all fish fed. Stimulus fish received the novel foods while still in their housing tanks. Each food was thawed and cut into pieces approximately 2 mm long, and around 2 g (wet mass) of either bloodworm or *Daphnia* was added to each tank. This volume provided an excess of food, and we distributed the food particles evenly across the tank bottom, ensuring that all individuals had access to it. Stimulus fish were allowed to feed for 1 h before the tests began, after which all uneaten food was siphoned from the bare glass substrate of their housing tanks. For each trial we formed two new stimulus shoals containing five fish fed on either diet, by randomly selecting one fish from each of the 10 housing tanks and placing them in the experimental tank, described below. After being used, the stimulus fish were added to one of two temporary housing tanks according to their diet, and at the end of the day of testing they were randomly reassigned (within their diet treatment) to the housing tanks.

The focal fish were drawn from a pool of around 125 individuals, from five of the housing tanks described above. These were rehoused as follows: 50 fish were divided equally between five 30-litre housing tanks, while the remaining 70 fish were held in two reserve tanks. On each day of testing, we randomly selected two fish from each of the five tanks containing 10 fish. Two further fish were then added to each tank from the reserve tanks, to maintain a constant density of 10 fish per housing tank. The selected focal fish were transferred as two groups of five, with fish from the same housing tanks separated, to two unfurnished 30-litre tanks, where they were fed 0.5 g of either experimental diet as described above. Drawing focal and stimulus fish from different holding tanks

allowed us to control for shoaling preferences based upon familiarity through individual recognition (Griffiths & Ward 2006). After testing, used focal fish were set aside in a 60-litre tank, so that no individual was used as a focal fish more than once at any point during the study. Further details of the treatment of the focal fish are given below.

Stimulus and focal fish were fed simultaneously and tested immediately afterwards. To move the fish between the feeding tanks and the experimental tanks we used small nets. We were careful to ensure that no debris such as uneaten food particles or faeces were moved between tanks, so that any diet-specific cues affecting the behaviour of the focal fish originated only from the stimulus fish themselves. Within each experiment, focal fish fed either diet were tested alternately, so that no two fish fed the same diet were tested immediately after one another, while the positioning of the stimulus fish was also altered between trials. After each set of 10 trials the water in the test tank was changed.

Ethical Note

The fish used in this study were captive bred and were obtained from a professional supplier. No fish died during the study period. No procedures required U.K. Home Office licensing. After the study the fish were retained in the laboratory to be used in future projects.

EXPERIMENT 1: STATIONERY SHOALS

Shoaling preferences based upon self-referent matching of resource cues have not previously been investigated in Whitecloud mountain minnows. For this reason we first sought to determine whether this species could discriminate between stationary stimulus shoals fed either the same or a different diet, before carrying out the subsequent experiments looking at group choice during shoal fission and prey patch selection, described below. We gave single focal fish a binary choice between shoaling with five stimulus fish fed the same diet as itself or five stimulus fish fed the alternative diet.

Methods

Apparatus

The experiment took place within a test tank measuring 90×30 cm and 30 cm high, with a water depth of 20 cm. The sides and rear of the tank were covered with black plastic sheeting, and observations were made through a slit in a black screen to minimize outside disturbance. Each stimulus shoal was housed within a mesh cylinder (12 cm in diameter, 22 cm tall) located 15 cm from either end of the tank. The mesh material was chosen to constrain the stimulus shoal in the appropriate region of the tank but allow olfactory cues to pass from them to the focal fish. We marked a circle around the base of each cylinder, 5 cm from its perimeter. This represented an association zone extending approximately two body lengths from the cylinder housing the stimulus shoal, within the

range of interindividual distances considered to constitute shoaling behaviour (Pitcher & Parrish 1993). Focal fish entering this area were considered to be shoaling with the stimulus fish.

Procedure

The stimulus fish were placed within each cylinder and allowed to settle for 5 min. The focal fish was then added to the centre of the test tank within a perforated clear plastic cylinder (10 cm in diameter). This allowed the focal fish to receive both visual and chemical cues from the two stimulus groups. The focal fish was held within the central cylinder for 5 min after which the cylinder was carefully raised and removed, releasing the focal fish and beginning the trial. The trial lasted for a further 5 min during which we recorded the total amount of time that the focal fish spent within the association zone of either stimulus group.

Statistical analyses

We analysed the shoaling preferences of the focal fish as follows: the amount of time that the focal fish spent shoaling with the stimulus group that had been fed the alternative diet was subtracted from the amount of time that it spent shoaling with the stimulus group that had been fed the same diet as itself, and compared against an expected value of zero using a Wilcoxon signed-ranks test. We analysed the pooled data from all of the focal fish fed each of the two diets, and also for each diet group separately. Finally, we used Mann–Whitney U tests to look for any differences in the shoaling preferences of the focal fish from each diet group. Statistical tests for all the experiments were two tailed.

Results

Focal fish showed a clear preference for shoaling with the stimulus group whose members had consumed the same diet as themselves (both diet groups pooled: Wilcoxon signed-ranks test: $Z = -3.77$, $N = 30$, $P < 0.001$; Fig. 1). This was true for both diet groups (bloodworm group: $Z = -2.35$, $N = 15$, $P = 0.019$; *Daphnia* group: $Z = -2.74$, $N = 15$, $P = 0.006$). A Mann–Whitney U test showed that there was no difference in the proportion of trial time that each diet group spent shoaling with its respective same diet stimulus shoal ($U = 93.5$, $N_1 = N_2 = 15$, $P = 0.43$). This suggests that the type of diet consumed by the focal fish did not affect its propensity to group with others fed the same diet.

EXPERIMENT 2: SHOAL FISSION

This experiment was designed to simulate a shoal fission event, in which a larger group of fish split into two smaller groups and moved apart to form two separate shoals. In this case the two smaller groups were composed of stimulus fish that had consumed the two different diets. A focal fish that had consumed one of the two diets was given the opportunity to follow one shoal or the other to

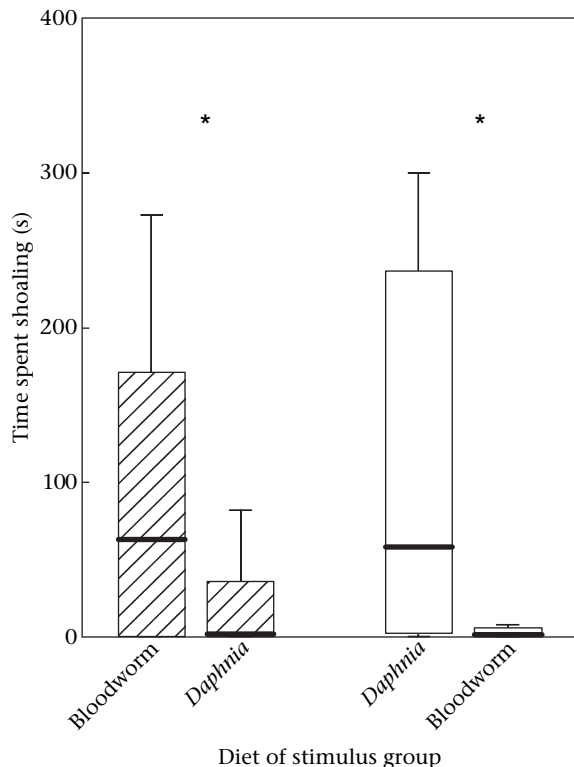


Figure 1. The median amount of time that focal fish spent shoaling with stimulus fish fed the same or an alternative diet to themselves. ▨: Focal fish fed bloodworm; □: focal fish fed *Daphnia*. The bold horizontal bars indicate the median value, the boxes show the interquartile range and the lower and upper error bars show the 5th and 95th percentiles. * $P < 0.05$.

one end of a large test tank. The apparatus used in the experiment was based upon that designed by Lachlan et al. (1998). We aimed to determine whether individual fish can use diet-specific cues to make rapid shoaling decisions under more naturally realistic conditions, when the stimulus groups are mobile and where group composition is unstable (Hoare et al. 2000).

Methods

Apparatus

The fish were tested in an experimental tank measuring 150×30 cm and 30 cm high, with a water depth of 20 cm. As in experiment 1, the sides and rear of the tank were covered with black plastic sheeting, and observations were made through a slit cut into a black screen. The stimulus and focal fish had been fed either bloodworm or *Daphnia* as described above. The two stimulus shoals were held within mesh cylinders (12 cm in diameter, 22 cm tall), through which olfactory cues could permeate. These were suspended 5 cm from the bottom of the tank from a cable which ran down the centre of the test tank along its longest axis from one end to the other. Each cylinder was attached to a towline, allowing them to be moved apart to either end of the tank.

Procedure

At the beginning of each trial the two cylinders that would contain stimulus shoals were placed side by side in the centre of the tank. The stimulus fish were added to these cylinders, while a single focal fish was then added to a third identical mesh cylinder placed on the floor of the tank immediately in front of, and in contact with, the two stimulus groups. Unlike the two cylinders housing the stimulus shoals, this one had an open bottom, allowing us to release the focal fish by raising the cylinder. All of the fish were allowed to settle for 5 min before the cylinder holding the focal fish was raised and removed, releasing the focal fish. The two cylinders housing the stimulus groups, each attached to a towline, were then immediately pulled along the overhead cable to either end of the test tank. Each was towed at a constant rate, so that it took 30 s to reach the end of the tank. This was approximately equal to the cruising speed of Whitecloud mountain minnows observed in their housing tanks, and was slow enough not to cause any obvious stress to either the stimulus fish inside the cylinders or the following focal fish. We marked vertical black lines on the outside of the tank 15 cm from either end. Focal fish that passed this line within 10 s of the stimulus shoal crossing it were considered to have followed that group. Focal fish that failed to pass either line within 10 s of the stimulus shoals crossing them were judged to have followed neither group.

Statistical analyses

We used binomial tests to compare shoal selection by the focal fish against a null expected distribution of 0.5. Focal fish that failed to approach either shoal were excluded from analyses. We analysed the pooled data from all of the focal fish fed each of the two diets, and also for each diet group separately.

Results

Significantly more focal fish followed the stimulus group whose members had consumed the same diet as themselves than followed the group that had been fed the alternative diet when the two moved apart (both diet groups pooled: binomial test: $N = 37$, $P = 0.001$; Fig. 2). In the trials where the focal fish had fed on bloodworm, 15 followed the bloodworm-fed stimulus group, but only three followed the *Daphnia*-fed group, with six failing to follow either ($N = 18$, $P = 0.008$). When the focal fish had fed on *Daphnia*, 14 followed the *Daphnia*-fed stimulus group, compared to five that followed the bloodworm-fed group, and five that failed to follow either, a difference that was marginally nonsignificant ($N = 19$, $P = 0.06$).

EXPERIMENT 3: PREY PATCH CHOICE

Individuals that identify, join and follow certain shoals are likely to come across and exploit the same resources as their shoalmates. In this experiment we sought to determine whether the diet-specific cues generated by the stimulus fish could influence prey patch selection in the focal fish receiving them.

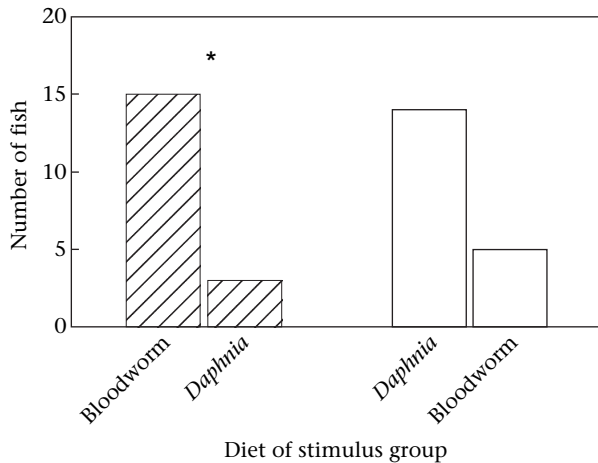


Figure 2. The number of focal fish that followed the stimulus group that had been fed the same or an alternative diet to themselves during a simulated shoal fission event. ▨: Focal fish fed bloodworm; □: focal fish fed *Daphnia*. * $P < 0.05$.

We gave single focal fish a binary choice between a prey patch containing a novel, neutral food located next to a stimulus shoal of five fish that had fed upon the same diet as they had and an otherwise identical prey patch located next to a shoal of stimulus fish that had been fed the alternative diet.

Methods

Apparatus

The layout of the experimental tank was the same as that used in experiment 1, with the exception that a prey patch was present immediately in front of each stimulus shoal. A clear plastic ring (6.5 cm in diameter) was attached to each of the mesh cylinders housing the stimulus fish. The rings were positioned so that they floated at the water's surface, 2 cm from either cylinder. A neutral food, freeze-dried *Tubifex* (Tetra GmbH, Herrenteich 78, 49324 Melle, Germany) were used as prey. Individual *Tubifex* were cut into pieces approximately 1 mm long and 0.25 g of these were floated on the water's surface within each of the two plastic rings, which prevented them from drifting around the tank. The focal fish was introduced to the centre of the test tank within a perforated clear plastic cylinder (10 cm in diameter).

Procedure

The stimulus fish were placed within their cylinders, while the focal fish was added to the centre of the test tank within its own cylinder. All fish were allowed to settle for 5 min. One minute before the focal fish was released the prey pieces were added to each prey patch. The cylinder holding the focal fish was then raised and removed, releasing the focal fish and beginning the trial. As in experiment 1 the trial lasted for 5 min during which we noted the first prey patch from which the focal fish fed, and the total number of prey pieces that it consumed from each patch. After every trial all of the uneaten food was removed from each prey patch.

Statistical analyses

We used binomial tests to compare first prey patch choice against a null expected distribution of 0.5. Focal fish that failed to approach either shoal were excluded from analyses. Prey patch use was analysed by comparing the difference between the number of prey pieces consumed from each prey patch against a null value of zero using a Wilcoxon signed-ranks test. We analysed the pooled data from all of the focal fish fed each of the two diets, and also for each diet group separately. Finally, we used Mann–Whitney U tests to look for any differences in the foraging rates of the focal fish from each diet group.

Results

Focal fish first fed from the prey patch located next to the stimulus group that had been fed the same diet as themselves on significantly more occasions than they did from the prey patch located next to the stimulus group that had been fed the alternative diet (both diet groups pooled: binomial test: $N = 27$, $P = 0.002$; Fig. 3).

In the trials where the focal fish were fed on bloodworm, nine first fed from the patch next to the bloodworm-fed stimulus group, four first fed from the patch next to the *Daphnia*-fed stimulus group, and two failed to feed at all ($N = 13$, $P = 0.27$). This nonsignificant difference may be attributed to a small sample size, and the relatively low statistical power of the binomial test. When the focal fish had fed on *Daphnia*, 13 first fed from the patch next to the *Daphnia*-fed stimulus group, compared to one individual that first fed from the patch next to the bloodworm-fed group, with one fish failing to feed from either ($N = 14$, $P = 0.002$).

Focal fish also consumed significantly more prey from the patch located closest to the stimulus group that had fed on the same diet as themselves (both diet groups

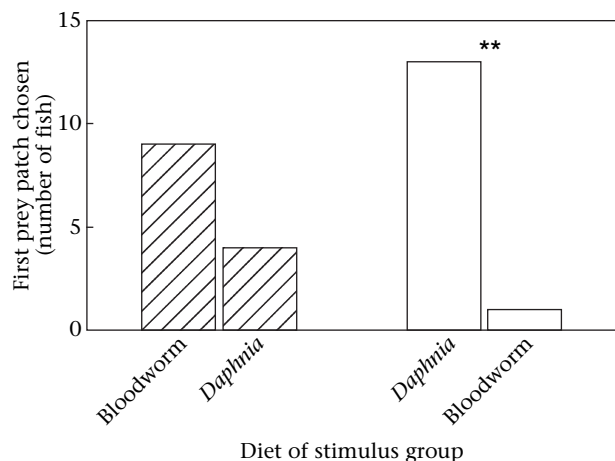


Figure 3. The number of trials in which the focal fish first fed from either the prey patch located next to the stimulus group that had been fed the same diet as themselves, or from an identical prey patch located next to the stimulus group that had been fed an alternative diet. The prey patches contained a neutral prey type. ▨: Focal fish fed bloodworm; □: focal fish fed *Daphnia*. ** $P < 0.005$.

pooled: Wilcoxon signed-ranks test: $Z = -2.21$, $N = 30$, $P = 0.02$; Fig. 4). This was also observed for both diet groups separately (bloodworm group: $Z = -2.03$, $N = 15$, $P = 0.02$; *Daphnia* group: $Z = -2.24$, $N = 15$, $P = 0.02$). The amount of prey consumed by the focal fish did not differ between those fed on the bloodworm or *Daphnia* diet (Mann–Whitney U test: $U = 78.00$, $N_1 = N_2 = 15$, $P = 0.35$).

DISCUSSION

In experiments 1 and 2 female Whitecloud mountain minnows detected differences in the prey use patterns of conspecifics, and preferentially shoaled with those that had recently consumed the same prey as themselves. These findings support similar ones reported for other, unrelated fish species (Olsen et al. 2003; Ward et al. 2004, 2005, 2007; Morrell et al. 2007; Webster et al. 2007, 2008), suggesting that self-referent matching of resource use patterns may be a general mechanism of social recognition in fishes.

Two of the key novel findings of this study (experiment 2) are that focal fish are able to discriminate between subsets of a larger stimulus shoal that have consumed different prey types, and that they can make rapid shoal choice decisions as the two subsets split into separate shoals and move apart. These findings build upon the knowledge gained from previous studies that considered only shoaling decisions made between static stimulus groups, by showing that embedded subgroups of individuals sharing patterns of resource use might remain

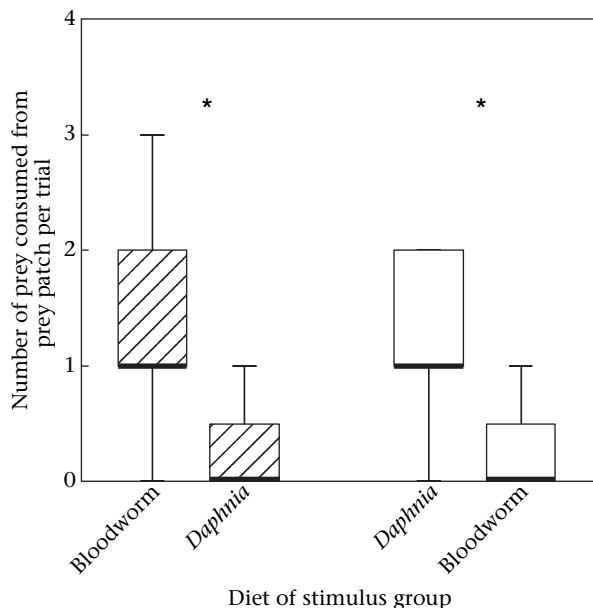


Figure 4. The median number of prey that focal fish consumed from each of two identical prey patches located next to either a stimulus group that had been fed the same diet as themselves, or a stimulus group that had been fed an alternative diet. The prey patches contained a neutral prey type. ▨: Focal fish fed bloodworm; □: focal fish fed *Daphnia*. The bold horizontal bars indicate the median value, the boxes show the interquartile range and the lower and upper error bars show the 5th and 95th percentiles. * $P < 0.05$.

together even under conditions where the composition of the larger shoal is subject to change through dynamic fission–fusion processes.

In experiment 3 we established that shoaling preferences based upon resource cues could influence prey patch choice, with focal fish being significantly more likely to feed from prey patches located close to shoals that had consumed the same diets as themselves. These findings suggest that resource cue matching can indirectly determine how individuals exploit their surroundings, affecting where they go and what they feed on.

The findings of experiment 3 reinforce the possibility that shoaling preferences based upon resource cue matching could facilitate the social learning of patch choices. This is one of the suggested, but hitherto untested, benefits to the individual of using this mechanism of social recognition (e.g. Webster et al. 2007). By shoaling with, and following, others, it is possible that the joining individual might come to learn the locations of patchily distributed resources, or routes of navigation, within the range of the group. Conceivably, via this mechanism individuals might acquire this information more rapidly or at lower risk than they would through private investigation of their surroundings. Moreover, this mechanism may constitute a short cut to individuals learning the location of new prey patches of their preferred type, known to other shoal members. A previous study from our laboratory established the plausibility of this argument. Lachlan et al. (1998) conducted a series of experiments in one of which focal guppies were given a binary choice of following moving shoals of numerically different sizes. They showed not only that focal individuals were more likely repeatedly to follow numerically larger shoals than smaller ones to a hidden food patch, but also that after following such a shoal to a given food patch several times, the same focal individuals were then able to locate the prey patch by themselves. This result shows that the focal fish was able to learn the location of the prey patch based upon its interactions with the group. The finding of our experiment 2, that resource cue matching influences which of two groups is followed, suggests that a similar mechanism of learning might be facilitated, something that is clearly worthy of further investigation.

Thus far we have considered the benefits to the joining individual of using resource-specific cues in deciding with whom to shoal. Intuitively it seems detrimental to the individual members of an established shoal to be joined by further individuals who are exploiting the same prey types, because they are direct competitors for what is likely to be a finite suite of resources. Viewed in this context, the joining individual might be regarded as an informational parasite, exploiting the information that the demonstrator fish have acquired through their own foraging efforts. However, there are also potential benefits to the individuals already established within the shoal from being joined by additional members who are exploiting the same resources as themselves. Joiners may also carry knowledge of prey patch locations that could supplement the knowledge within the group, while the established group members can also benefit from fresh social information generated by newer members. Larger

groups tend to find patchily distributed prey more rapidly than smaller groups (Pitcher et al. 1982), and newcomers to an established group could therefore increase the rate of prey detection of the group as a whole, something that potentially benefits its constituent individuals by providing them with the opportunity to scrounge from or kleptoparasitize one another. In addition, members of larger groups bear lower per capita predation risks as a result of attack dilution and predator confusion effects (Krause & Ruxton 2002). These benefits might outweigh the costs of increased competition for prey in environments where predation risk is intense. Finally, groups composed of individuals with similar resource use patterns shoal more cohesively (Webster et al. 2007), providing them with further antipredatory benefits. Ultimately, the balancing point between the costs and benefits to established group members of being joined by further individuals will be determined by a range of environmental pressures, including resource density and distribution, and predation pressure.

Clearly, selection has favoured the ability in some fishes to detect patterns of resource use in others, to assess these relative to their own patterns of resource use, and to base behavioural strategies around them. Resource competition is a major constraint upon individual fitness (Ward et al. 2006) and under conditions where it is detrimental to an individual to be joined by others that are likely to compete directly with it for resources, we might predict that counteradaptations will arise, influencing how and when fishes produce resource-specific cues. In fact, the question of whether individuals can actively modulate the resource cues that they produce may be moot, since the physiological mechanisms by which they are assimilated, processed and transmitted, and whether individuals have any active control over how they are accrued and released, are not yet known. Fishes are known to gather information about the sex, degree of relatedness and hierarchical standing of conspecifics (Bryant & Atema 1987; Thom & Hurst 2004) using chemical cues derived from their urine (Moore et al. 1994), faeces (Courtenay et al. 1997) and external mucous coating (Matsumura et al. 2004). It is possible that prey-specific cues might also be transmitted via these channels. Further work in this area would be useful, if we are to gain a better understanding of the physiological mechanisms that underpin this form of social information.

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