

*Département de Biologie, Université de Moncton, Moncton*

## **Food-anticipatory Activity as a Cue for Local Enhancement in Golden Shiners (Pisces: Cyprinidae, *Notemigonus crysoleucas*)**

STEPHAN G. REEBBS & BRUNO Y. GALLANT

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### **Abstract**

The goal of this study was to test whether food-anticipatory activity, which is more subtle than feeding activity, can be used as a cue for local enhancement by fish. Golden shiners, *Notemigonus crysoleucas*, were offered a choice between spending time near a shoal of conspecifics normally fed at that time of day or a shoal normally fed at another time. Despite the fact that no food was delivered during the tests, the shoal that was normally fed at that time had more fish moving and more fish close to the surface, where food usually appeared, than the other shoal. This is evidence of food-anticipatory activity. The choosing shiners, after being deprived of food for 24–48 h, preferred to stay near the anticipating shoal rather than near the other one. When satiated, the shiners chose both shoals at random, indicating that hunger promotes the use of food-anticipatory cues in shoal choice and local enhancement. The results also support the idea that food-anticipatory activity can attract competitors for food and may therefore be costly. Food-anticipatory activity might also attract predators, but the fact that satiated shiners did not actively avoid anticipating shoals indicates that the potential cost of predator attraction would be either low or mitigated by other factors.

Corresponding author: Stephan G. REEBBS, Département de Biologie, Université de Moncton, Moncton, New Brunswick, Canada E1A 3E9. E-mail: reebbs@umoncton.ca

### **Introduction**

If food always becomes available at the same time every day, animals can learn the significance of this time of day and anticipate its occurrence (MISTLBERGER 1994). This anticipation can be measured through behaviour. Examples include bees flying to a food dish a few minutes before a sugar solution is made available (BELING 1929; WAHL 1932; MOORE et al. 1989), fish becoming more mobile a few hours before mealtime (DAVIS & BARDACH 1965; SPIELER & NOESKE 1984), and various mammals, laboratory rats in particular, wheel-running or bar-pressing more during the hour that precedes a regular meal (MISTLBERGER 1994). Food-anticipatory activity is presumably advantageous for animals in nature, inasmuch as it allows them to be first to get to the food. Time discrimination can also allow them to avoid foraging at times that are unlikely to provide a reward (HALL et al. 1979; DAAN 1981; RIJNSDORP et al. 1981).

Food-anticipatory activity may also have costs, however. One potential cost is that the behaviour might be used as a cue by individuals that have not learned the relationship

between food arrival and time of day but that can join experienced animals so as to share or steal their food. It is well known that animals can observe the behaviour of feeding or foraging individuals and join these foragers, a phenomenon called 'local enhancement' (HINDE & FISHER 1951) or 'forage area copying' (KREBS et al. 1972). (Similar concepts exist for within-group interactions: producer-scrounger systems, information-sharing systems, and bird roosts or colonies being used as information centres; GRIER & BURK 1992.) In birds, previous demonstrations of local enhancement have involved the presence or absence of flocks as cues (KREBS 1974; WAITE 1981). In contrast, previous studies on fish have looked at direct feeding and food-discovery behaviour as cues (PITCHER & HOUSE 1987; KRAUSE 1992; RYER & OLLA 1992). Food-anticipatory activity, on the other hand, has never been studied. This type of activity is more subtle than feeding behaviour, consisting mostly of increased mobility and orientation towards the potential sources of food. The question then is, can subtle food-anticipatory activity be used as a cue for local enhancement?

We investigated this question with a cyprinid fish, the golden shiner, *Notemigonus crysoleucas*. This is a strongly shoaling species in which scramble competition predominates (there is no aggression amongst shoalmates), and therefore there is good potential for local enhancement in this species. Golden shiners can also learn to associate various places and times of day with food arrival (REEBS 1996), which suggests that they have good potential for food-anticipatory activity.

We performed two experiments. In the first one, we verified that golden shiners can anticipate the arrival of food, and then asked whether a hungry fish can discriminate between anticipating and non-anticipating shoals and spend more time near the former. We measured fish mobility and fish position within the aquarium as possible parameters of anticipation, and we offered test fish a choice between a shoal always fed at that time of day and another shoal always fed at another time. In the second experiment, we asked whether shoal choice by the test fish is hunger dependent. A hungry fish may focus on the anticipatory behaviour of its conspecifics with a view to join them, but in contrast a well-fed fish may prefer to avoid an anticipating group. The reason behind this avoidance by satiated fish would be related to another potential cost of food-anticipatory activity: predation risk. Anticipating shoals probably pay more attention to food and are therefore less vigilant for predators, and they exhibit behaviour (e.g. more movement) that is likely to increase detection by predators. Fish might therefore incur a significant predation risk in such a group, and because a well-fed individual would not need to be with a shoal that expects food anyway, it should avoid it and join another, non-anticipating one instead.

## Experiment 1

### Material and Methods

Golden shiners 5.6–9.8 cm in total length were minnow-trapped in Folly Lake, 12 km south of Moncton, New Brunswick, throughout the summer of 1996. They were brought to the laboratory and kept in large aquaria (140 × 30 × 45 cm) for at least 2 wk before the start of experimentation. Water temperature in the aquaria was  $15 \pm 2^\circ\text{C}$ . Lighting came from windows in the room. Fish were fed a maintenance diet of commercial flakes at regular intervals throughout the day. These flakes were delivered by automatic feeders at the surface of the water.

Tests took place in a separate windowless room where overhead fluorescent lights maintained a photoperiod

of 12 h (lights on at 0800 h). The experimental set-up consisted of two large aquaria (140 × 30 × 45 cm) placed face to face. The back aquarium was completely divided into right and left halves by an opaque plexiglass partition. Each half contained a stimulus shoal, and these two shoals were fed at different daily times. The front aquarium contained a test fish which could move from side to side. A camera placed in front of this set-up allowed us to record the behaviour of the test fish and the two shoals at the same time. A mirror angled at 45° above the front aquarium enabled us to distinguish the test fish from the stimulus fish.

Each stimulus shoal was made up of four fish matched for size within 1 cm of total length. Every day for at least 2 wk, one shoal received food flakes at the surface, from an automatic feeder, every 30 min between 1000 and 1200 h, whereas the other shoal was fed every 30 min between 1600 and 1800 h. About 24 h before each test, cardboard was placed between the two aquaria to isolate them visually, and a test fish, matching the size of the shoal fish but selected from a different storage tank, was placed in the front aquarium without access to food. The next day, the automatic feeders above the shoals were disconnected and the cardboard was removed at 0900 h (i.e. 1 h before the normal feeding time of the morning-fed shoal). The behaviour of the test fish and of both stimulus shoals was then recorded for 2 h. (This period was therefore made up of 1 h prior to the normal feeding time of the morning-fed shoal, and 1 h during which the shoal would have been fed had the feeders been operating; for the afternoon-fed shoal, this period was 5–7 h prior to their normal feeding time.) This was a 'morning test'.

At the end of a morning test (1100 h), the feeders were reconnected, the cardboard was put back in place, and the test fish was removed. At 1500 h, a new test fish was put in the front aquarium. The next day, feeders were disconnected at 1500 h, the cardboard was removed, and the behaviour of the test fish and both stimulus shoals was recorded for 2 h. This time period therefore comprised 1 h preceding the normal feeding time of the afternoon-fed shoal, and 1 h during which they would have received food had the feeders been operating; for the morning-fed shoal, this period was 3–5 h past their last (and normal) feeding time. This was an 'afternoon test'.

This procedure was repeated once with the same stimulus shoals. The shoals were then replaced with new ones which were trained for 2 wk. If the previous morning-fed shoal had been on the left side of the aquarium, the new one was put on the right side, and vice versa. Two morning and two afternoon tests were conducted with these new shoals. Stimulus shoals were then changed again, and so on until 16 morning and 16 afternoon tests had been conducted.

Videotapes were viewed on fast-forward to measure the percentage of time spent by the test fish in the half of the aquarium facing each stimulus shoal. The tapes were also viewed for 5 s at 5-min intervals, and we noted the number of stimulus fish that moved more than one body length during the 5 s, as well as the number of fish in the top half of the tank. With the mean of all 12 measurements per hour, we obtained an index of activity and proximity to the surface (where food normally arrived) for each stimulus shoal. If anticipatory behaviour was present, we would expect more fish from the morning-fed shoal to be active and close to the surface in the morning, as compared with the afternoon-fed shoal. The situation would be reversed in the afternoon. We tested this prediction with nested ANOVA, comparing morning and afternoon-fed shoals while nesting the pair of tests that came from each individual shoal (SOKAL & ROHLF 1981). We also counted the number of tests when the shoal that was expected to anticipate had higher values than the other one, and submitted the resulting proportion to a binomial test (CONOVER 1980). Significance level was set at  $p = 0.05$ .

If hungry test fish can detect a difference between an anticipating shoal and a non-anticipating one, we would expect more of them to spend more time near the morning-fed shoal on morning tests, and near the afternoon-fed shoal on afternoon tests. This expectation was checked with binomial tests (CONOVER 1980).

All of the above predictions should hold for the total duration of a given test (2 h), but we analysed the data from each hour separately. Hereafter, we designate each hour by its starting time (e.g. hour 9 means the 1-h period from 0900 to 1000 h).

## Results

As expected, during the morning tests, more morning-fed fish were active and in the upper half of the aquarium than afternoon-fed fish, while the reverse was true during the afternoon tests (Fig. 1). This is evidence that golden shiners can anticipate food arrival (hours 9 and 15) and that anticipatory behaviour persists during the normal time of food delivery (hours 10 and 16) even when food is not delivered. This behaviour was qualitatively

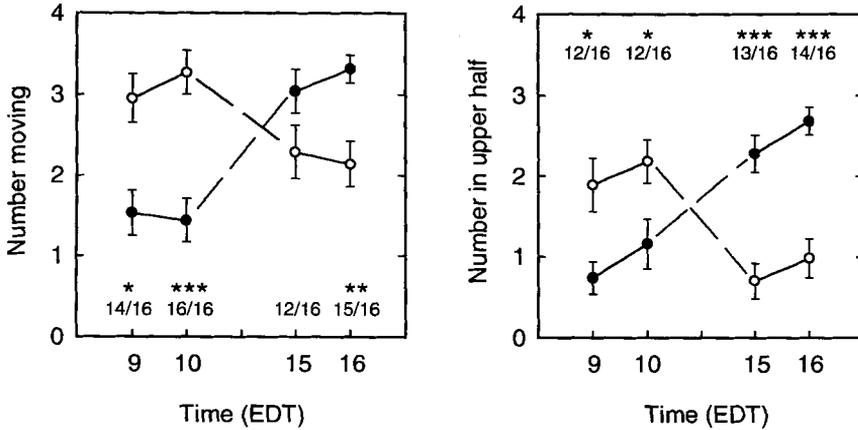


Fig. 1: Mean ( $\pm$  SE,  $n = 16$ ) number of fish, within a shoal of 4, moving in the aquarium or present in its upper half at different times of day in the absence of food delivery. Open symbols indicate shoals normally fed at the surface in the morning (1000–1200 h), while filled symbols indicate shoals normally fed in the afternoon (1600–1800 h). Asterisks show times when significant differences were found between morning-fed and afternoon-fed shoals (nested ANOVAs, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.005$ ). Data came from shoal choice tests given to single fish that had been food-deprived for 24 h. Quotients show the proportion of tests when the shoal that was normally fed at that particular time of the day had higher values than the other shoal. On a binomial test, proportions of 12/16 or higher have p-values of 0.04 or less

different from feeding activity; the fish did not dart towards the surface or stay close to it like they normally did when food flakes appeared. They were simply moving more and staying more in the upper half of the water column.

There was no evidence that test fish preferred the anticipating group during the morning tests. During hour 9, only 9 out of 16 test fish spent more time near the morning-fed group ( $p = 0.40$ ); during hour 10, only 6 out of 16 fish did so ( $p = 0.89$ ). Overall (all fish and both hours combined), test fish spent  $48 \pm 35$  (SD)% of their time on the side of the morning-fed fish.

However, test fish did prefer the anticipating group during the afternoon tests. During both hours 15 and 16, 12 out of 16 test fish spent more time near the afternoon-fed shoal ( $p = 0.04$ ). Overall, test fish spent  $67 \pm 35\%$  of their time near the anticipating group. This value climbs to  $85 \pm 20\%$  if only the 12 fish that chose the anticipating group are considered.

### Discussion

Our results indicate that food-anticipatory activity can be present in golden shiners, and that it can be measured through an increase in activity and a more frequent proximity to the surface if the food normally appears there. REEBS (1996) also gave some evidence that golden shiners could anticipate food arrival: the fish moved ahead of time to the aquarium half (left or right) where food normally arrived. In the present experiment, food-

anticipatory activity appeared at least 1 h before the normal feeding time, but no more than 6 h, at least in the case of the afternoon-fed fish (on Fig. 1, values are low for the afternoon-fed fish at hour 10, i.e. 5–6 h before their normal feeding time). In the mummichog, *Fundulus heteroclitus*, DAVIS & BARDACH (1965) measured increases in activity that anticipated food arrival by various amounts of time, most often 2–4 h, and seldom more than 6 h. Similar results were obtained by SPIELER & NOESKE (1984) in their work on goldfish, *Carassius auratus*.

Is this anticipatory activity a direct consequence of hunger or the manifestation of a circadian mechanism? Our experiments did not address this question, but we have observed that fish activity decreases back to normal levels after the usual feeding time even when food is not delivered (unpubl. data), eliminating the possibility of direct hunger effects. Whatever the answer, the difference between anticipating and non-anticipating shoals was real and offered a potential cue for the test fish to discriminate between the two.

The preference tests, however, yielded ambiguous results. Fish did prefer the anticipating group in afternoon tests, but they chose randomly during the morning tests. A possible explanation for this discrepancy lies in the exact difference between the two shoals in terms of their last feeding times. At the beginning of the morning tests, the morning-fed and afternoon-fed shoals had last been fed 21 h ago and 15 h ago, respectively. For the afternoon tests, these values were 3 h and 21 h, respectively. (The difference is linked to the presence or absence of night between the test and the last feeding time.) These numbers reveal a greater contrast between the two shoals during the afternoon tests, and although this did not translate into a greater difference in activity level and only a somewhat greater difference in fish position (Fig. 1), our test fish may have detected the contrast in other ways unknown to us (the polarization, density and swimming speed of the shoal are possibilities: ROBINSON & PITCHER 1989).

Another possible explanation resides in the motivation to feed by test fish. Fish may pay more attention to food-anticipatory activity if they are hungrier. If the fish have an endogenous rhythm of feeding activity peaking in the afternoon, they may prefer food-anticipating shoals more clearly at that time. However, we have no evidence to either confirm or deny that such a rhythm in feeding activity exists in golden shiners (examples of such rhythms in other fish species kept under laboratory conditions: WRIGHT & EASTCOTT 1982; BOUJARD et al. 1992; BOUJARD 1995; SÁNCHEZ-VAZQUEZ et al. 1995a,b, 1996). Nevertheless, the possibility of hunger levels affecting our results remains interesting, and we tested it in the next experiment by comparing test fish that were either satiated or deprived of food for 48 h.

## Experiment 2

### Material and Methods

Procedures were similar to those of experiment 1, except that the aquaria were smaller (75 × 30 × 45 cm), and the tests were shorter and limited to part of the 2 h during which the shoals were normally fed. Cardboard was placed between the front and back aquaria at 1000 hours (as before, the morning-fed shoals normally received food between 1000 and 1200 h, although no food was delivered during the tests). A test fish that had been starved for 48 h in a separate tank was placed in the front aquarium. At 1030 h, the cardboard was removed and the behaviour of the starved fish, as well as that of the shoals, was recorded for 30 min. At 1100 h, the cardboard

was put back in place, and the starved test fish was replaced by a fish that had just been fed to satiation in a separate tank. At 1130 h, the cardboard was removed and the behaviour of the satiated fish and shoals was recorded, again for 30 min. At 1200 h, the test fish was removed, and the morning shoal was fed. This was a pair of morning tests. On a subsequent day, the procedure was repeated with new test fish between 1600 and 1800 h (a pair of afternoon tests).

These pairs of morning and afternoon tests were repeated once with the same shoals but with new test fish, satiated fish this time being tested before starved ones. The shoals were then replaced with others that were trained for 2 wk. This cycle went on until 12 satiated and 12 starved fish had been tested in both the morning and the afternoon.

Videotapes were analysed in the same manner as before. A new consideration was to compare satiated and starved fish. We did this through  $\chi^2$  tests on the number of test fish (satiated or starved) that spent more time near a given shoal (anticipating or not). We also used Mann-Whitney tests (SPSS-PC, version 3.0) to compare the percentage of time spent near the anticipating shoal by satiated and starved fish.

## Results

There was evidence that shoals could anticipate the arrival of food under the new protocol. According to binomial tests and nested ANOVAs, the shoal that was expected to anticipate had significantly more fish moving than the other shoal (upper panels of Fig. 2).

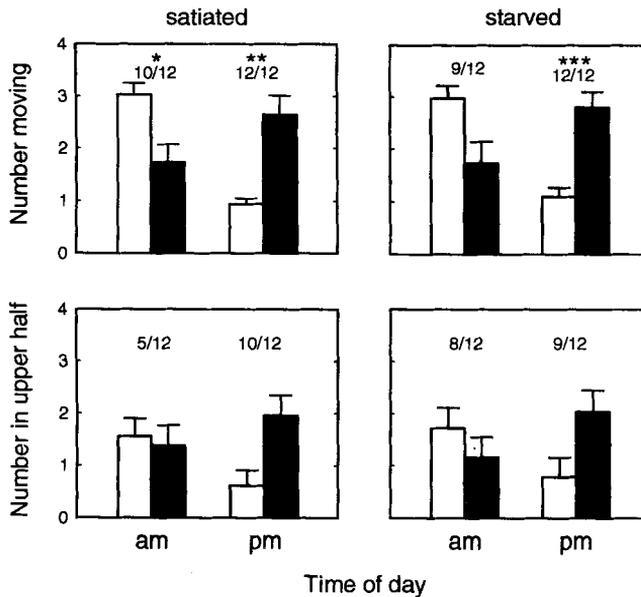


Fig. 2. Mean ( $\pm$  SE,  $n = 12$ ) number of fish, within a shoal of 4, moving in the aquarium or present in its upper half at different times of day (am = 1000–1200 h, pm = 1600–1800 h) in the absence of food delivery. Open bars indicate shoals normally fed in the morning (1000–1200 h), while filled bars indicate shoals normally fed in the afternoon (1600–1800 h). Asterisks show times when significant differences were found between morning-fed and afternoon-fed shoals (nested ANOVAs, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.005$ ). Data came from shoal choice tests given to single fish that were either satiated (left panels) or food-deprived for 48 h (right panels). Quotients indicate the proportion of tests when the shoal normally fed at that particular time of the day had higher values than the other shoal. On a binomial test, proportions of 9/12 or higher have  $p$ -values of 0.07 or less

According to binomial tests (but not ANOVAs), the shoal that was expected to anticipate also had significantly more fish in the upper half of the aquarium during the afternoon tests, but not during the morning (lower panels of Fig. 2). The left and right panels on Fig. 2 show almost identical results, and therefore satiated and starved fish were faced with similar choices.

During the morning tests, 11 of 12 starved fish spent more time near the morning-fed shoal ( $p = 0.003$ ). In contrast, satiated fish showed no preference: half of the 12 fish preferred one shoal and half preferred the other ( $p = 0.61$ ). This difference between starved and satiated fish is significant on a  $\chi^2$  test ( $p = 0.025$ ). On average, starved and satiated fish spent  $60 \pm 9\%$  and  $50 \pm 18\%$  of their time, respectively, near the morning-fed shoal. The difference between these two values was almost significant ( $Z = 1.67$ ,  $p = 0.09$ ).

During the afternoon tests, 11 of 12 starved fish spent more time near the afternoon-fed shoal ( $p = 0.003$ ). Again, the satiated fish showed no significant preference: 4 of 12 spent more time near the afternoon-fed group ( $p = 0.19$ ). On a  $\chi^2$  test, this difference between starved and satiated fish is significant ( $p = 0.003$ ). On average, starved and satiated fish spent, respectively,  $60 \pm 11\%$  and  $51 \pm 28\%$  of their time near the afternoon-fed shoal. This difference, however, was not significant on a Mann–Whitney U-test ( $Z = 1.33$ ,  $p = 0.18$ ).

### Discussion

Starved fish showed a consistent preference for the anticipating shoal, while satiated fish did not. As compared with our previous experiment, the starved fish had been deprived of food for longer (48 h instead of 24 h) and their preference for the anticipating shoal was more marked (11/12 as against 12/16); moreover, this preference occurred on both morning and afternoon tests, as opposed to the afternoon only in the previous experiment. Taken together, these results strongly suggest that hunger promotes the use of anticipatory behaviour as a cue for shoal choice and local enhancement.

The fact that Mann–Whitney tests did not detect significant differences between starved and satiated fish in the percentage of time spent near the anticipating shoal was related to the high variability shown by the satiated fish. Only in this group did we see high percentages of time spent near either shoal. Preference for the anticipating shoal (percentage over 50) by satiated fish did not occur often, but most of these percentages were high and outranked the more numerous values from the starved fish, leading to non-significant or only near-significant differences between starved and satiated fish. This does not detract from our previous conclusion about the existence of a preference in hungry fish and its direction. It simply indicates that hungry fish tended to examine the two shoals extensively, whereas satiated fish did not.

As a group, satiated fish did not prefer the anticipating shoal, but contrary to our expectation they did not avoid it either. Their choice appeared random. This suggests that no selective pressure has pushed fish to recognize movement and proximity to the surface on the part of their shoalmates as a cause of predation risk for the satiated individual. This does not mean that movement and proximity to the surface do not attract predators. It may simply be that the satiated fish can itself remain immobile, vigilant and deeper in the water than its shoalmates, which may draw predator attention onto themselves rather than

on the satiated individual. However, this is not an entirely satisfactory hypothesis; because of lower detectability in quiet shoals, we should still expect an individual fish to do better in the company of quiet conspecifics than with food-anticipating ones. Once a food-anticipating shoal is detected, the satiated individual's chance of being captured may be smaller than that of its shoalmates, but it would be smaller still had the shoal not been detected in the first place. At Folly Lake, birds appear to be the only predators of golden shiners (pers. obs.), and birds most likely use fish movement and proximity to the surface to detect their prey.

Another possibility to explain the lack of avoidance on the part of the satiated fish is that they did not feel threatened by predators in our laboratory situation. However, this explanation suffers from the fact that, in previous work from this laboratory, satiated shiners preferred to associate with larger shoals made up of individuals with body size that matched that of the choosing fish (REEBS & SAULNIER, 1997). Preference for larger shoals and avoidance of the 'oddity effect' are consistent with protection from predators. Why would satiated shiners show choices consistent with predator avoidance in those situations but not in the present one? Nevertheless, it might pay to conduct further experiments where test fish are given a choice between anticipating and non-anticipating shoals, both in the presence and absence of a potential predator (HAGER & HELFMAN 1991).

A final explanation is that, in the smaller aquaria used in this second experiment, satiated test fish could position themselves in such a way as to observe both the anticipating and non-anticipating groups, and therefore did not need to associate closely with any of them to benefit from whatever information (food or predator detection) could be gleaned from them. However, almost all test fish stayed close to the glass next to the back aquarium, a place where it was impossible to get a view of both shoals simultaneously.

It may simply be unreasonable to expect a fish to avoid shoals that are anticipating food arrival, even if the fish is satiated. Golden shiners probably spend most of their lives in shoals, and these groups have to feed regularly. If a satiated individual was prompted to leave a shoal every time its less fortunate shoalmates are foraging or expecting to feed, it would keep shuttling back and forth between groups. Such a fish would lose the benefits of familiarity with its shoalmates (for an example of such benefits, see CHIVERS *et al.* 1995).

### Concluding Discussion

Our results show that fish, if properly motivated (*i.e.* hungry), can use subtle behavioural cues in conspecifics to join these other fish and increase their own chances of obtaining food. The exact nature of these cues remains uncertain, and it may prove difficult to differentiate the various effects of increased mobility, orientation towards the source of food, swimming speed, shoal polarization and shoal density, given that all these variables often covary. But whatever the cues, their presence in food-anticipating fish entails a cost in the possible recruiting of other fish which may share the food.

This cost may be mitigated by the limited range at which the cues are detectable. If the cues are purely visual, their effective recruiting range will depend on the turbidity of the water. In most natural habitats, where visibility is limited, visually based local enhancement would probably be confined to within-shoal recruitment. Only if two shoals came in

close contact could one of them be induced to join with the other if the latter showed food-anticipatory behaviour. Of course, cues could also be olfactory or auditory, in which case their range of action might be greater, but this remains to be investigated.

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### Literature Cited

- BELING, I. 1929: Über das Zeitgedächtnis der Bienen. *Z. Vergl. Physiol.* **9**, 259—338.
- BOUJARD, T. 1995: Diel rhythms of feeding activity in the European catfish, *Silurus glanis*. *Physiol. Behav.* **58**, 641—645.
- , MOREAU, Y. & LUQUET, P. 1992: Diel cycles in *Hoplosternum littorale* (Teleostei): entrainment of feeding activity by low intensity colored light. *Env. Biol. Fishes* **35**, 301—309.
- CHIVERS, D. P., BROWN, G. E. & SMITH, R. J. F. 1995: Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. *Can. J. Zool.* **73**, 955—960.
- CONOVER, W. J. 1980: *Practical Nonparametric Statistics* (2nd Ed.). John Wiley & Sons, New York.
- DAAN, S. 1981: Adaptive daily strategies in behavior. In: *Handbook of Behavioral Neurobiology*, Vol. 4: *Biological Rhythms* (ASCHOFF, J., ed.). Plenum Press, New York. pp. 275—298.
- DAVIS, R. E. & BARDACH, J. E. 1965: Time-co-ordinated prefeeding activity in fish. *Anim. Behav.* **13**, 154—162.
- GRIER, J. W. & BURK, T. 1992: *Biology of Animal Behavior* (2nd Ed.). Mosby Year Book, St Louis, MO.
- HAGER, M. C. & HELFMAN, G. S. 1991: Safety in numbers: shoal size choice by minnows under predatory threat. *Behav. Ecol. Sociobiol.* **29**, 271—276.
- HALL, D. J., WERNER, E. E., GILLIAM, J. F., MITTELBAACH, G. G., HOWARD, D. & DONER, C. G. 1979: Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). *J. Fish. Res. Board Can.* **36**, 1029—1039.
- HINDE, R. A. & FISHER, J. 1951: Further observations on the opening of milk bottles by birds. *Brit. Birds* **44**, 393—396.
- KRAUSE, J. 1992: Ideal free distribution and the mechanism of patch profitability assessment in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behaviour* **123**, 27—37.
- KREBS, J. R. 1974: Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). *Behaviour* **51**, 100—131.
- , MACROBERTS, M. H. & CULLEN, J. M. 1972: Flocking and feeding in the great tit, *Parus major*: an experimental study. *Ibis* **114**, 507—530.
- MISTLBERGER, R. E. 1994: Circadian food-anticipatory activity: formal models and physiological mechanisms. *Neurosci. Biobehav. Rev.* **18**, 171—195.
- MOORE, D., SIEGFRIED, D., WILSON, R. & RANKIN, M. A. 1989: The influence of time of day on the foraging behavior of the honeybee, *Apis mellifera*. *J. Biol. Rhythms* **4**, 305—326.
- PITCHER, T. J. & HOUSE, A. C. 1987: Foraging rules for group feeders: area copying depends upon food density in shoaling goldfish. *Ethology* **76**, 161—167.
- REEBS, S. G. 1996: Time-place learning in golden shiners (Pisces: Cyprinidae). *Behav. Proces.* **36**, 253—262.
- & SAULNIER, N. 1997: The effect of hunger on shoal choice in golden shiners (Pisces: Cyprinidae, *Notemigonus crysoleucas*). *Ethology* **103**, 642—652.
- RIJNSDORP, A., DAAN, S. & DIJKSTRA, C. 1981: Hunting in the kestrel, *Falco tinnunculus*, and the adaptive significance of daily habits. *Oecologia* **50**, 391—406.
- ROBINSON, C. J. & PITCHER, T. J. 1989: The influence of hunger and ration level on shoal density, polarization and swimming speed of herring, *Clupea harengus* L. *J. Fish Biol.* **34**, 631—633.
- RYER, C. H. & OLLA, B. L. 1992: Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. *Anim. Behav.* **44**, 69—74.
- SÁNCHEZ-VAZQUEZ, F. J., MADRID, J. A. & ZAMORA, S. 1995a: Circadian rhythms of feeding activity in sea

- bass, *Dicentrarchus labrax* L.: dual phasing capacity of diel demand-feeding pattern. *J. Biol. Rhythms* **10**, 256—266.
- , —, —, IIGO, M. & TABATA, M. 1996: Demand feeding and locomotor circadian rhythms in the goldfish, *Carassius auratus*: dual and independent phasing. *Physiol. Behav.* **60**, 665—674.
- , ZAMORA, S. & MADRID, J. A. 1995b: Light-dark and food restriction cycles in sea bass: effect of conflicting zeitgebers on demand-feeding rhythms. *Physiol. Behav.* **58**, 705—714.
- SOKAL, R. R. & ROHLF, F. J. 1981: *Biometry* (2nd Ed.). W.H. Freeman, San Francisco.
- SPIELER, R. & NOESKE, T. A. 1984: Effects of photoperiod and feeding schedule on diel variations of locomotor activity, cortisol, and thyroxine in goldfish. *Trans. Am. Fish. Soc.* **113**, 528—539.
- WAHL, O. 1932: Neue Untersuchungen über das Zeitgedächtnis der Bienen. *Z. Vergl. Physiol.* **16**, 529—589.
- WAITF, R. K. 1981: Local enhancement for food finding by rooks (*Corvus frugilegus*) foraging on grassland. *Z. Tierpsychol.* **57**, 15—36.
- WRIGHT, D. E. & EASTCOTT, A. 1982: Operant conditioning of feeding behaviour and patterns of feeding in thick lipped mullet, *Crenimugil labrosus* (Risso) and common carp, *Cyprinus carpio* (L.). *J. Fish Biol.* **20**, 625—634.

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