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Assessing the Ideal Free Distribution: Do Guppies Use Aggression as Public Information about Patch Quality?

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Abstract

Aggression can be costly to foragers, yet some recent research suggests that foragers should use aggression as a cue to patch quality (the attractive aggression hypothesis). If aggression is predictive of patch quality, then the attractive aggression hypothesis predicts that the distribution of foragers should follow the distribution of aggression. If, instead, aggression is repulsive because it is costly, then the distribution of foragers should diverge from the distribution of aggression. We tested the attractive aggression hypothesis using female guppies, *Poecilia reticulata*, and found that the distribution of foragers followed the distribution of food, but was unaffected by the distribution of aggression. These data do not support the attractive aggression hypothesis, but instead suggest that the distribution of aggression is a consequence of the distribution of foragers, and that aggression is not used as public information about patch quality.

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Introduction

When faced with patches of unknown quality, social foragers have access to two sources of information: personal sample information and public information. Personal sample information is acquired by personally sampling the patch. Public information is acquired from the behaviour of other animals (Valone 1989). When using public information a forager can sample a patch by observing the behaviour of other foragers (Templeton & Giraldeau 1996). These two sources of information are not mutually exclusive.

When resources are patchily distributed in the environment, Fretwell & Lucas (1970) predicted that animals would distribute themselves according to the resource distribution in what they called an ideal free distribution (IFD). IFD theory

assumes that foragers have perfect information and that all foragers compete on an equal basis. However, even when these assumptions are known to be violated, foragers are still capable of conforming to the resource distribution (Milinski 1988; Milinski & Parker 1991), although not always (Kennedy & Gray 1993). The question is why do foragers do so well? What information do foragers use to assess patch quality? The more information an animal has access to, the better its ability to perceive differences in patch quality (Koops 1998). Thus, foragers that use public information can increase their ability to assess patch quality, and should be able to exhibit closer conformity to an IFD.

The idea that foragers can use public information to assess patch quality has a long history in the IFD literature. For example, Harper (1982) found that mallard ducks, *Anas platyrhynchos*, were initially misled by the rate of food input when he changed the size of food items. This suggests that ducks foraging in one patch could acquire information about the rate of food input in the other patch, either from seeing the food enter the patch (thrown by the experimenter) or from the behaviour of other foraging ducks. Milinski (1984), finding no change in the time it took groups to reach the IFD when he changed the timing of food input, concluded that three-spined sticklebacks, *Gasterosteus aculeatus*, did not acquire information from one another. We know that foragers are attracted to the foraging (Krause 1992) and anticipatory (Reebs & Gallant 1997; Lachlan et al. 1998) activity of conspecifics, but this does not mean they use this information to assess the quality of patches. Gotceitas & Colgan (1991) found that three-spined sticklebacks prevented from personally sampling a patch failed to choose the more profitable patch, instead preferring the patch with more conspecifics.

Experimental results from Pitcher et al. (1982) and Pitcher & Magurran (1983) suggest that goldfish, *Carassius auratus*, and European minnows, *Phoxinus phoxinus*, can use information from other members of a foraging group. In these experiments, however, all members were able to forage freely. The ability to acquire personal sample information seems to be important. Pitcher & House (1987) found that when goldfish were able to acquire food in low quantity, they used information from successfully foraging conspecifics, but when no food was available, they ignored public information.

Kennedy & Gray (1994) proposed that foragers use aggressive interactions as information about the quality of patches. When the quality of a food patch increases, aggressive interactions tend to increase; therefore, aggression could be a reliable predictor of patch quality and aggression would be attractive. They tested their hypothesis with mallard ducks, manipulating the distribution of aggressive interactions by increasing the size of food items, while keeping the total food per trial constant. When food occurred in large items, the distribution of aggressive interactions was a better predictor of resource distribution, and the mallards exhibited closer conformity to the IFD.

Attraction to aggression is surprising. Aggression is generally considered to be costly because it can lower food discovery rates through interference, incur time and energy costs, and increase the risk of injury and predation. Given the potential costs of aggression, it is equally reasonable for foragers to avoid patches with more

aggressive interactions (repulsive aggression). Alternatively, the distribution of aggression may be a result of the distribution of foragers, and have nothing to do with patch assessment (neutral aggression).

When testing the attractive aggression hypothesis, Kennedy & Gray (1994) used the distribution of aggressive interactions as the source of public information about patch quality. However, the distribution of aggressive interactions will be influenced by the distribution of foragers, and there is no way to tell whether aggressive interactions influence the distribution of foragers, or whether foragers influence the distribution of aggressive interactions. Therefore, there is no reason to expect the distribution of aggressive interactions to provide any more information about patch quality than the distribution of foragers. Alternatively, if aggression does provide public information about patch quality, then per capita aggression (aggressive interactions per forager) controls for the distribution of foragers. According to the attractive aggression hypothesis, a change in the distribution of per capita aggression should change the distribution of foragers.

Here we present a test of Kennedy & Gray's (1994) attractive aggression hypothesis using female guppies, *Poecilia reticulata*. Female guppies have been shown to conform more closely to an IFD than males, because they refine their assessment of patch quality over time (Abrahams 1989). Male guppies, however, appear to be less concerned with the distribution of food than females. Female guppies have also been shown to learn foraging information from other female guppies (Laland & Williams 1997; Lachlan et al. 1998), suggesting that they could use public information for patch assessment.

To test the attractive aggression hypothesis, we manipulated the distribution of per capita aggression. We did this by providing food at two sources: one spatially dispersed and the other spatially concentrated. According to resource defence theory, concentrating food in space should increase aggressive interactions, while dispersing food in space should decrease aggressive interactions (see Grant 1993 for a review). When food is dispersed broadly at the rich patch and concentrated at the poor patch, the distribution of per capita aggression should provide a poor indication of the distribution of food as there will be relatively more aggression where there is relatively less food. When food is concentrated at the rich patch and dispersed at the poor patch, the distribution of per capita aggression should provide a good indication of the food distribution as there will be relatively more aggression where there is relatively more food. By always providing food through both sources, but reversing their value, we attempted to manipulate the distribution of per capita aggression without affecting total aggression levels. If foragers use aggression as public information about patch quality, then changing the distribution of per capita aggression should result in a corresponding change in the distribution of foragers.

Materials and Methods

Seven groups of 10 female guppies (weight: $\bar{x} = 0.196$ g, $SD = 0.045$, $n = 4$; length: $\bar{x} = 21.57$ mm, $SD = 1.82$, $n = 4$), *Poecilia reticulata*, from a lowland sec-

tion of the Quaré River in Trinidad were placed in 38-l aquaria ($50 \times 26.5 \times 29$ cm). Food was provided at two ends of the tank, ≈ 40 cm apart, through feeders that passively drained into the tank (see Abrahams 1989 for a complete description of the feeders). Each feeder provided freshly hatched, live brine shrimp, *Artemia salina*, nauplii and eggs. A total of $125 \mu\text{l}$ of brine shrimp (≈ 170 animals) were divided between the two feeders each morning (AM trial) and afternoon (PM trial) in one of five food ratios: 5:1, 2:1, 1:1, 1:2, or 1:5. Two different food delivery ends were attached to the feeders: a bar that spread the food over 20 cm from five equidistant holes, and a point source that pushed the food up from the bottom of the tank through a single hole. We subjected each group to two different treatments: the bar-rich treatment, where the rich patch provided food through the bar while the poor patch provided food through the point source, and the point-rich treatment, where the rich patch provided food through the point source while the poor patch provided food through the bar. When neither patch was richer (the 1:1 food ratio), the location of the point and bar were randomly determined by a coin toss. Each group experienced all five food ratios in random order in each of the two treatments. The order of treatments was balanced across groups. Each food ratio was provided for 1 d, morning and afternoon, with each feeding lasting 15 min. Spatial distribution data were collected on each group every 30 s for 15 min. The total number of aggressive interactions over the 15-min trial was recorded at each feeder.

To analyse the distribution of aggressive interactions, we used per capita aggression to remove any effect of forager distribution (as observed by Kennedy & Gray 1994) and to control for the possibility that there are more aggressive interactions at a site simply because there are more foragers, as fish can be attracted to a site based on the number of conspecifics (e.g. Gotceitas & Colgan 1991). By spatially concentrating food at the point source, we should be increasing the per capita aggression in this patch creating a positive relationship between the distribution of per capita aggression and the distribution of food. When the bar source is rich, this relationship should be negative. We started our analysis by testing for a change in the distribution of per capita aggression between the bar-rich and point-rich treatments.

Because we were interested in the ability of foragers to assess the distribution of resources (R), we limited our analysis of the spatial distribution of foragers to the last 5 min of the trial. The per capita aggression was calculated for the entire trial as the number of interactions in a patch (I) divided by the number of foragers at the patch (N). All seven groups experienced all five food ratios in both treatments, so data on the distribution of per capita aggression, $\text{Log} [(I_1/N_1)/(I_2/N_2)]$, and foragers, $\text{Log} (N_1/N_2)$, were analysed using an analysis of variance with repeated measures (ANOVAR). Factors included in the analysis were: a. treatment, to test for a difference between the point-rich and bar-rich treatments; b. food ratio, $\text{Log} (R_1/R_2)$, to test for an effect of the distribution of food; and c. the treatment-by-food-ratio interaction. If we observe a difference in the distribution of per capita aggression between the point-rich and bar-rich treatments, then the attractive aggression hypothesis predicts: i. a similar difference between the treatments in the

distribution of foragers; and ii. that the distribution of foragers should be more extreme in the point-rich treatment than the bar-rich treatment, i.e. the slope of $\text{Log}(N_1/N_2)$ against $\text{Log}(R_1/R_2)$ should be higher in the point-rich treatment.

Results

To test the attractive aggression hypothesis, we needed to affect the distribution of per capita aggression without changing the overall aggression levels (Kennedy & Gray 1994). We observed no difference in the total aggression levels between the point-rich ($\bar{x} = 61.46$, $SD = 17.29$) and the bar-rich ($\bar{x} = 72.00$, $SD = 19.75$) treatments (paired $t_6 = 1.37$, $p = 0.22$, $\beta = 0.79$). The total number of foragers actively feeding during the trials did differ between the bar-rich ($\bar{x} = 9.60$, $SD = 0.38$) and the point-rich ($\bar{x} = 9.25$, $SD = 0.61$) treatments (paired $t_6 = 2.97$, $p = 0.025$); however, the per capita aggression levels did not differ (paired $t_6 = 1.10$, $p = 0.31$, $\beta = 0.85$; bar-rich: $\bar{x} = 7.47$, $SD = 1.92$; point-rich: $\bar{x} = 6.62$, $SD = 1.68$). Therefore, we conclude that our manipulation did not change aggression levels and that any change in the distribution of foragers can be due to changes in available information and not increased total aggression. There was also no evidence that the repeated-measures design led to any habituation or the formation of dominance hierarchies (Fig. 1).

The distribution of per capita aggression during the AM trials was not influenced by treatment alone (ANOVAR: $F_{1,6} = 0.37$, $p = 0.57$, $\beta = 0.92$), nor was it influenced by food ratio alone (ANOVAR: $F_{4,24} = 1.41$, $p = 0.26$, $\beta = 0.63$). However,

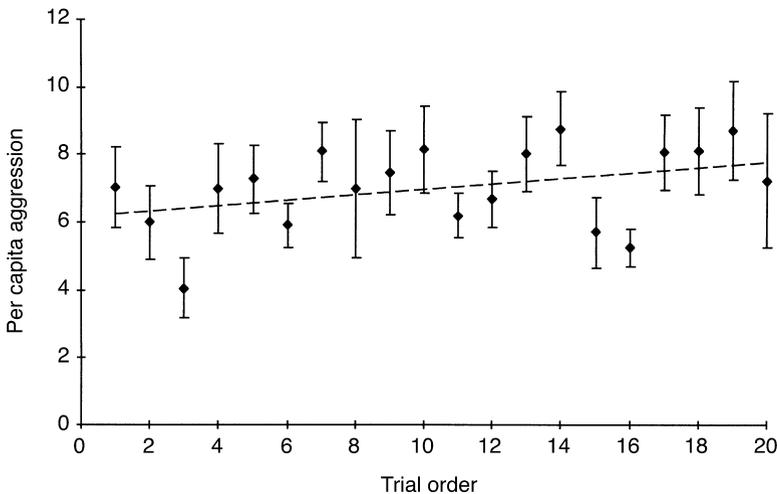


Fig. 1: Mean (± 1 SE, $n = 7$) per capita aggression in each of the 20 trials (two treatments \times five food ratios \times two trials per day) experienced by each group, showing no evidence of habituation or the formation of dominance hierarchies

there was a significant interaction between treatment and food ratio (Fig. 2a, ANOVA: $F_{4,24} = 3.84$, $p = 0.015$). Thus, our experimental manipulation did change the distribution of per capita aggression during the AM trials. This effect was lost by the PM trials (ANOVA: treatment: $F_{1,6} = 3.22$, $p = 0.12$, $\beta = 0.67$; food ratio: $F_{4,24} = 2.45$, $p = 0.07$, $\beta = 0.40$; treatment \times food ratio: $F_{4,24} = 1.57$, $p = 0.21$, $\beta = 0.59$). We are interested in how foragers assess the IFD, and the attractive aggression hypothesis proposes a mechanism by which animals may assess the distribution of food in their environment. This assessment will occur during the initial exposure to a novel food distribution, so we restricted our analyses to the AM data only.

The distribution of foragers was not significantly affected by the treatment (ANOVA: $F_{1,6} = 0.054$, $p = 0.82$, $\beta = 0.95$), nor was there any treatment-by-food-ratio interaction (ANOVA: $F_{4,24} = 1.84$, $p = 0.15$, $\beta = 0.52$). However, the distribution of foragers was significantly affected by the distribution of food (Fig. 2b, ANOVA: $F_{4,24} = 49.57$, $p < 0.001$) as predicted by the IFD. Furthermore, in complete opposition to the attractive aggression hypothesis, the distribution of foragers was more extreme in the point-rich treatment than the bar-rich treatment in only one of seven groups (sign test: $p = 0.12$).

Discussion

Guppies do not appear to use the distribution of per capita aggression as public information about patch quality. Patches with a relatively higher level of aggression are not attractive. This suggests that female guppies ignore aggression when making patch choice decisions. By using per capita aggression as our measure, we removed the causation problem faced by Kennedy & Gray (1994), and the change in the distribution of aggression could not have been caused by any change in forager distribution. Thus, this is the first true test of the attractive aggression hypothesis, and there is no evidence to support the idea that animals use aggression as public information.

A potential criticism of the current experiment is the low power. In our experiment, low power was caused by high variance (see Fig. 2a and the analysis of per capita aggression levels). For the attractive aggression hypothesis to work, a strong correlation must exist between aggression levels and food availability. Due to high variance, our data demonstrate no such correlation and further suggest that there is little information about resource availability associated with aggression.

It is possible that in manipulating the spatial distribution of food, we created a monopolizable resource at the point source, thereby removing any effect of aggression as public information. While we did see greater per capita aggression at the point source, as predicted by resource defence theory (Grant 1993), this did not translate into a change in the distribution of foragers. If the point source had been monopolized, we should have seen extreme undermatching in the point-rich treatment and overmatching in the bar-rich treatment. This was not the case

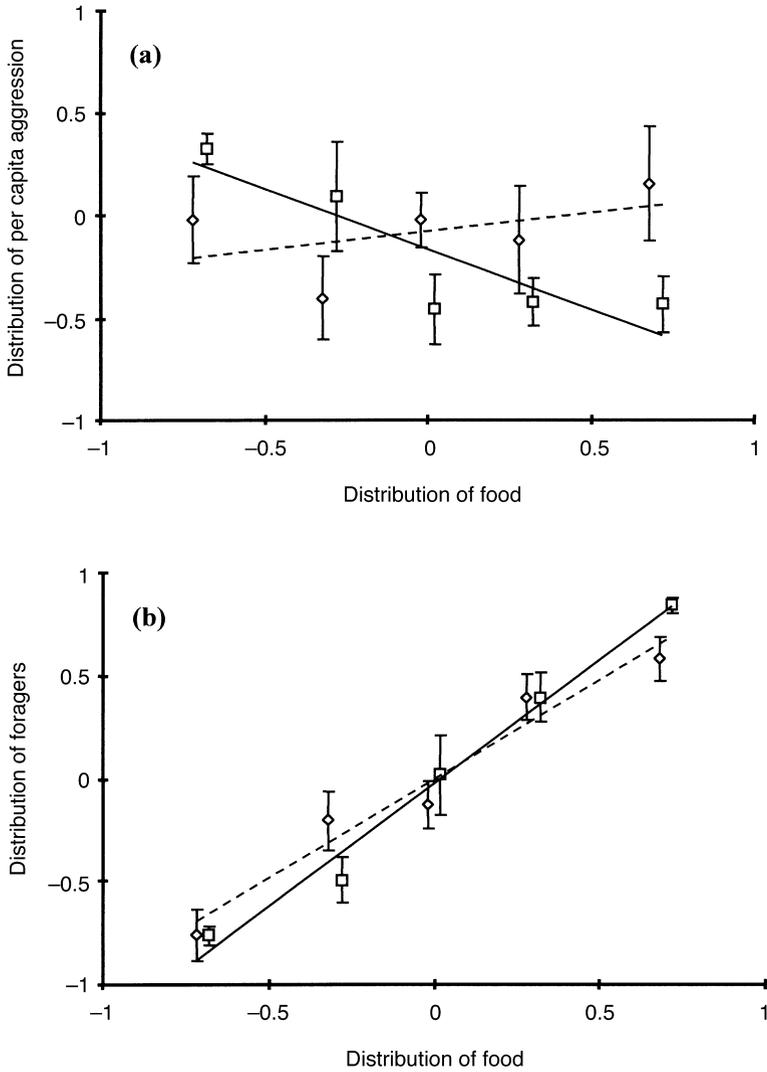


Fig. 2: Distribution of: a. per capita aggression, $\text{Log} [(I_1/N_1)/(I_2/N_2)]$; and b. foragers, $\text{Log} (N_1/N_2)$, as a function of the distribution of food, $\text{Log} (R_1/R_2)$, in the bar-rich and point-rich treatments. Bar-rich data are represented by a solid line and square symbols. Point-rich data are represented by a dashed line and diamond symbols. The ideal free distribution (IFD) predicts a slope of one for the distribution of foragers. The distribution of foragers (y) as a function of one of the distribution of food (x) in the bar-rich treatment is described by the line: $y = -0.001 + 1.20x$, and in the point-rich treatment by the line: $y = -0.02 + 0.97x$. All data are offset for clarity of presentation

(Fig. 2b). Although there was a trend in this direction in six of the seven groups, the deviation from an IFD was not extreme in either treatment.

It is also possible that by using a repeated-measures design, groups had the opportunity to establish stable dominance hierarchies with low levels of aggression. We found no evidence that stable dominance hierarchies were established (Fig. 1), and the experimental design did not reduce aggression levels. Furthermore, Kennedy & Gray (1994) reported average aggression levels of 0.07 aggressive interactions/mallard/min. In our experiment, aggression levels were six times greater than this at 0.44 and 0.5 aggressive interactions/guppy/min in the point-rich and bar-rich treatments, respectively. So, the availability of public information through aggressive interactions was not limited in our experiment.

Schooling in fish can provide antipredator benefits through the confusion effect. However, the effectiveness of the confusion effect is reduced when individuals in the group stand out (Landeau & Terborgh 1986; Theodorakis 1989). Huntingford (1982) proposed that aggression levels should be reduced in schools that experience higher predation pressure and Magurran & Seghers (1991) found support for this hypothesis in populations of wild guppies. If aggression is to be used to assess patch quality, it is presumably because it is easier to perceive a difference between patches based on aggression levels than intake rates. If aggression levels are reduced in guppy schools due to predation pressure, then the difference in aggression between patches may be insufficient for foragers to perceive a difference, and thus, aggression would fail to relieve the perceptual constraint faced by foraging guppies (Abrahams 1986; Koops 1998). However, as already discussed, aggression levels were not reduced in this experiment, so perceptual constraints do not explain the lack of evidence for the attractive aggression hypothesis.

Is it possible that guppies do not use public information at all? Valone & Giraldeau (1993) found that budgerigars, *Melopsittacus undulatus*, ignored public information when making patch departure decisions. However, Templeton & Giraldeau (1995) found that European starlings, *Sturnus vulgaris*, do use public information. We expect life history to affect the value of information (Koops & Abrahams 1998), and information with the same reliability will sometimes be used or ignored based on the benefits and costs of information and misinformation (Koops 1998). However, various species of fish have been shown to use information acquired from conspecifics when making foraging decisions (Pitcher et al. 1982; Pitcher & Magurran 1983; Pitcher & House 1987; Krause 1992; Reeb & Gallant 1997), including guppies (Laland & Williams 1997; Lachlan et al. 1998). Guppies also exhibit mate copying (e.g. Dugatkin 1992; Dugatkin & Godin 1993) which is the use of public information about mates (Nordell & Valone 1998). The fact that guppies do not use aggression as public information does not mean that guppies do not use public information.

Reeb & Gallant (1997) showed that hungry golden shiners, *Notemigonus crysoleucas*, cued into the food-anticipatory behaviour of conspecifics when making patch choice decisions. However, the behavioural cue that is actually used is unknown. Reeb & Gallant (1997) did find that golden shiners preferred conspecifics exhibiting more movement and less resting behaviours. Various species of

birds have also been shown to use coarse-level local enhancement when choosing foraging locations (Poysa 1992). If aggression is associated with activity, so that groups with greater levels of activity also exhibit greater levels of aggression, then Kennedy & Gray's (1994) finding that the distribution of aggression influences the distribution of foragers would be a result of the correlation between aggression and activity. Instead of using aggression, ducks may be cueing into the anticipatory behaviour of conspecifics, and Kennedy & Gray (1994) failed to tease apart the influence of activity and aggression.

Conclusions

While Kennedy & Gray (1994) concluded that mallards use aggression as a cue to patch quality, our study suggests that guppies do not. The present results, together with Kennedy & Gray's (1994) use of aggressive interactions instead of per capita aggression, suggest that aggression is a consequence of the distribution of foragers. There is no evidence that aggression is used as public information about patch quality.

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Literature Cited

- Abrahams, M. V. 1986: Patch choice under perceptual constraints: a cause for departures from an ideal free distribution. *Behav. Ecol. Sociobiol.* **19**, 409–415.
- Abrahams, M. V. 1989: Foraging guppies and the ideal free distribution: the influence of information on patch choice. *Ethology* **82**, 116–126.
- Dugatkin, L. A. 1992: Sexual selection and imitation: females copy the mate choice of others. *Am. Nat.* **139**, 1384–1389.
- Dugatkin, L. A. & Godin, J.-G. J. 1993: Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behav. Ecol.* **4**, 289–292.
- Fretwell, S. D. & Lucas, H. L. 1970: On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**, 16–36.
- Gotceitas, V. & Colgan, P. 1991: Assessment of patch profitability and ideal free distribution: the significance of sampling. *Behaviour* **119**, 65–76.
- Grant, J. W. A. 1993: Whether or not to defend? The influence of resource distribution. *Mar. Behav. Physiol.* **23**, 137–153.
- Harper, D. G. C. 1982: Competitive foraging in mallards: 'ideal free' ducks. *Anim. Behav.* **30**, 575–584.
- Huntingford, F. A. 1982: Do inter- and intraspecific aggression vary in relation to predation pressure in sticklebacks? *Anim. Behav.* **30**, 909–916.
- Kennedy, M. & Gray, R. D. 1993: Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. *Oikos* **68**, 158–166.
- Kennedy, M. & Gray, R. D. 1994: Agonistic interactions and the distribution of foraging organisms: individual costs and social information. *Ethology* **96**, 155–165.
- Koops, M. A. 1998: Misinformation and assessment uncertainty in the ecology of information use. PhD thesis, Univ. of Manitoba, Winnipeg.

- Koops, M. A. & Abrahams, M. V. 1998: Life history and the fitness consequences of imperfect information. *Evol. Ecol.* **12**, 601—613.
- Krause, J. 1992: Ideal free distributions and the mechanism of patch profitability assessment in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behaviour* **123**, 27—37.
- Lachlan, R. F., Crooks, L. & Laland, K. N. 1998: Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Anim. Behav.* **56**, 181—190.
- Laland, K. N. & Williams, K. 1997: Shoaling generates social learning of foraging information in guppies. *Anim. Behav.* **53**, 1161—1169.
- Landeau, L. & Terborgh, J. 1986: Oddity and the 'confusion effect' in predation. *Anim. Behav.* **34**, 1372—1380.
- Magurran, A. E. & Seghers, B. H. 1991: Variation in schooling and aggression amongst guppy (*Poecilia reticulata*) populations in Trinidad. *Behaviour* **118**, 214—234.
- Milinski, M. 1984: Competitive resource sharing: an experimental test of a learning rule for ESSs. *Anim. Behav.* **32**, 233—242.
- Milinski, M. 1988: Games fish play: making decisions as a social forager. *Trends Ecol. Evol.* **3**, 325—330.
- Milinski, M. & Parker, G. A. 1991: Competition for resources. In: *Behavioural Ecology: an Evolutionary Approach*, 3rd edn (Krebs, J. R. & Davies, N. B., eds). Blackwell Sci. Publ., Oxford, pp. 137—168.
- Nordell, S. E. & Valone, T. J. 1998: Mate choice copying as public information. *Ecol. Letts* **1**, 74—76.
- 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.
- Pitcher, T. J. & Magurran, A. E. 1983: Shoal size, patch profitability and information exchange in foraging goldfish. *Anim. Behav.* **31**, 546—555.
- Pitcher, T. J., Magurran, A. E. & Winfield, I. J. 1982: Fish in larger shoals find food faster. *Behav. Ecol. Sociobiol.* **10**, 149—151.
- Poysa, H. 1992: Group foraging in patchy environments: the importance of coarse-level local enhancement. *Ornis. Scand.* **23**, 159—166.
- Reebs, S. G. & Gallant, B. Y. 1997: Food-anticipatory activity as a cue for local enhancement in golden shiners (Pisces: Cyprinidae, *Notemigonus chrysoleucas*). *Ethology* **103**, 1060—1069.
- Templeton, J. J. & Giraldeau, L.-A. 1995: Patch assessment in foraging flocks of European starlings: evidence for the use of public information. *Behav. Ecol.* **6**, 65—72.
- Templeton, J. J. & Giraldeau, L.-A. 1996: Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. *Behav. Ecol. Sociobiol.* **38**, 105—114.
- Theodorakis, C. W. 1989: Size aggregation and the effects of oddity on predation risk in minnow schools. *Anim. Behav.* **38**, 496—502.
- Valone, T. J. 1989: Group foraging, public information, and patch estimation. *Oikos* **56**, 357—363.
- Valone, T. J. & Giraldeau, L.-A. 1993: Patch estimation by group foragers: what information is used? *Anim. Behav.* **45**, 721—728.

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