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A test of the ideal free distribution with unequal competitors

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Summary. The distribution of goldfish differing in competitive status approximately mimicked that expected for the ideal free distribution but with slightly too many fish in the poorer site. As predicted by phenotype-limited game theory models of dispersion, the mean rank of fish in a site varied inversely with the number of fish, both in the high and low input sites, and there was no correlation between competitive rank and time spent in the better site. The intake was higher for each individual in the high input site than in the low input site, showing that the distribution was not an exact evolutionarily stable strategy. We suggest that the deviation is due to sampling or perceptual constraints. Analysis of other studies with continous input shows that the discrepancy from the theoretical expectation increases with input ratio.

Introduction

The ideal free distribution describes the behaviour of competing individuals given a choice of sites (Fretwell and Lucas 1970). It assumes all individual are equal and that individuals distribute themselves such that each obtains the same intake. There has been considerable interest in testing the Ideal Free Distribution (Courtney and Parker 1985; Davies and Halliday 1979; Godin and Keenleyside 1984; Harper 1982; Milinski 1979; Parker 1970, 1974; Thornhill 1980; Whitham 1980). However, many of the published tests state that there were consistent differences between individuals and this violates the basic assumption of the Ideal Free Distribution. Game theory models which incorporate individual differences (Sutherland and Parker 1985; Parker and Sutherland 1986) entail determining the evolutionary stable strategy (ess) for each phenotype whilst taking into account the distribution of all other phenotypes.

Sutherland and Parker (1985) and Parker and Sutherland (1986) showed that it is important to distinguish between interference studies, in which the presence of conspecifics reduces intake by interference, and continuous input studies, in which food arrives continuously and individuals scramble to obtain as large a share as possible. Both the predictions of the models and the results from published research differ between these two types of study. In this paper we test the predictions of the models of continuous input.

The main assumptions of continuous input models are that competitive differences exist between phenotypes, that payoffs of a given competitor are always reduced by the addition of more competitors to a site and that the relative payoffs of phenotypes do not change between sites. The model describing the ess showed that there is a range of possible solutions in which the sums of the competitive abilities are held in fixed proportion to the input rate at a site (Parker and Sutherland 1986). For example, suppose good competitors do twice as well as poor competitors at all sites. The various solutions for a given input rate include a number of good competitors in the site (say 4) or twice as many poor competitors (8) or a range of intermediate combinations (3 good and 2 poor, 2 good and 4 poor, 1 good and 6 poor). A specific form of this prediction, which we test here, is that mean competitive rank of animals at a site should be inversely correlated with the number of animals at that site (Prediction 1). At the ESS, the intake of a given phenotype should be equal at all sites. We test this prediction by comparing the intake of individuals at sites differing in input rate and number of competitors (Prediction 2).

Methods

We used 10 cm long goldfish *Carassius auratus* because it is easy to recognise individuals by their natural colour variation and they are suitable for studying foraging behaviour in patchy environments (Lester 1984). A 60 × 30 × 30 cm tank was used at ambient temperature (19.0–19.8° C). The food items were tubifex worms which were dropped in singly using tweezers. Each fish gained experience of feeding on tubifex worms for 1 min, twice a day, for 14 days prior to the experiment. Once a day they were fed *ad libitum* on commercial flake food. To minimise disturbance the room was darkened and the sides and back of the tank were covered. The behaviour and intake rate of all fish were recorded with a video camera and the data extracted during playback.

The same approach was used to determine both the competitive ability of each individual and the distribution of individuals. The fish were given a choice of food input rate at the two ends of the aquarium; either one item every ten seconds (high input) or one item every twenty seconds (low input). The positions of high and low input were alternated in each trial. A line was drawn midway down the tank and every ten seconds the position of each fish was recorded during the 10 min trial. The intake of each fish was also noted. Seven fish were used. Each trial involved six fish and every combination of fish was used.

Results

Practically all the prey items introduced (98.4%) were consumed immediately. Competitive ability was assessed by calculating the average intake rate for individuals whilst in the presence of both 3 and 4 fish in the high input site and determining the mean of the two figures. This measure is correlated with the values for the average intake rate on all occasions ($r_s = 0.857$, $P < 0.05$) but ensures that the measure is not confounded by input rate or number of fish present.

The mean number of fish was 3.48 ± 0.04 in the high input site and 2.52 ± 0.04 in the low input site whilst the ideal free distribution without unequal competitors predicts 4 in the high and 2 in the low input sites. The ratio varied between trials with the extremes being 3.15:2.85 and 2.23:3.76. The ratio changed little during a trial and, if anything, deviated further below a 4:2 ratio with time (r_s of ratio against minute $= -0.588$, NS). Similarly the ratio deviated further away from a 4:2 ratio with the sequence of trials. Thus, there is no evidence that fish were learning between or within experiments in a way that would result in a closer fit to the expected distribution.

There were marked differences in intake between individual fish and these differences were consistent between trials (ANOVA $F = 4.90$, $P < 0.001$). The persistent differences between individuals show that the ideal free distribution does not apply, even though the ratios are approximately those predicted by the ideal free model. For each individual the sequence in which the trials took place had no effect on intake rate (ANOVA $F = 0.297$, NS). As in the study by Milinski (1984), there was no relationship between competitive rank and the percentage of time spent in the better site ($r_s = -0.036$, NS).

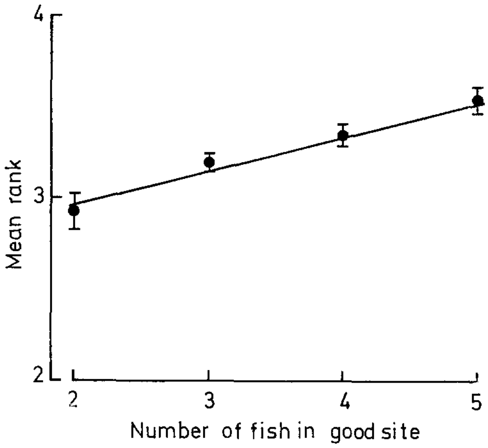

Fig. 1. Mean rank of individuals (±1 standard error) plotted against number of individuals in the high input site (ANOVA $F = 28.52$, $P < 0.001$)

Milinski (1984) found a relationship between the number of switches and rank. Such a relationship is expected when the mean rank varies inversely with the number of individuals. In this study the relationship between the number of switches per trial and rank was poor (ANOVA $F = -2.79$, $P = 0.087$) but the two lowest competitors switched significantly more often than the rest (mean per trial 9.25 v 5.03, $t = 2.87$, $P < 0.01$).

The ratio of the number of fish in the good: poor site varied between the extremes of 5:1 and 1:5 in the experiment as a whole. This variation could either (1) be due to the fish failing to conform to the expectations of the phenotype limited ESS model, for example due to sampling constraints, or (2) conform with the predicted range of possible solutions to the ess model. In accordance with this latter possibility we can show that the mean rank of fish correlated inversely with the number of fish in both the high and low input sites (conforming with Prediction 1, Fig. 1). This pattern was highly significant (low input site ANOVA $F = 16.19$, $P < 0.001$: high input site ANOVA $F = 28.52$, $P < 0.001$). However, the average intake was higher for each individual when it fed in the high input site than when it fed in the low input site (contradicting Prediction 2, Table 1).

Milinski (1986) found that the poorest competitors provided the worst fit to the Ideal Free Distribution and in our study the poorer competitors showed little difference in intake between the two sites (Table 1). However the time spent in each site was unaffected by rank (see previous paragraph) so the differences seem to be due to differing abilities in exploiting patches.

Table 1. Average intake rate (intake per 10 s spent in that site) of individual fish in the two sites. The intake is consistently higher in the high input site (paired *t*-test = 2.97, $P < 0.05$)

Rank	High input	Low input
1	0.411	0.260
2	0.459	0.182
3	0.309	0.026
4	0.307	0.232
5	0.298	0.227
6	0.102	0.075
7	0.031	0.030

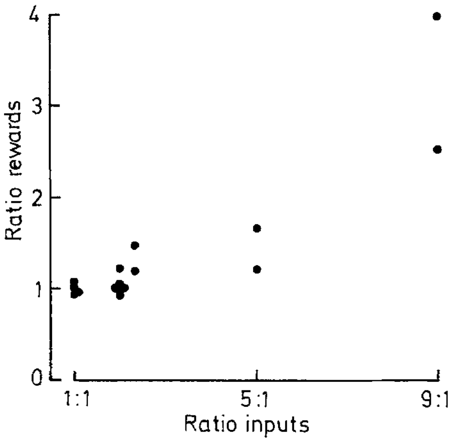

Fig. 2. The relationship between the ratio of the input rates in two sites and the ratio of rewards in the two sites. Each data point relates to a separate experiment ($r_S = 0.788$, $P < 0.001$). The rewards are determined from the average distribution once an equilibrium had been reached. Data were extracted from Godin and Keenleyside (1984), Harper (1982), Milinski (1979), Milinski (1984), Shingler (1985) and the current study

Discussion

This study shows that two phenomena are important in the distribution of the goldfish. As predicted from the game theory models of dispersion with continuous resource input there are a range of solutions in which the number of individuals at a site is related to their rank, with mean rank varying inversely with number of fish in both high and low input sites. However, the fit to the model is not perfect since each individual had a greater intake in the high input site. This runs contrary to the expectation of the ESS models because all individuals would be able to gain by spending more time in the high input site. It seems likely that this discrepancy is due to sampling or perceptual constraints.

Other studies have usually found that more individuals occur in the poorer sites than expected (Abrahams 1986). A review of all the published studies of continuous input, in which intake rates can be assessed, shows that the discrepancy from the predicted distribution depends upon the degree of inequality in the input rates (Fig. 2, $r_s = 0.788$, $P < 0.001$). If the input rates differ considerably between the sites then the animals spend too long in the low input sites. Such a result would be expected from models of perceptual constraints (Abrahams 1986).

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References

Abrahams MV (1986) Patch choice under perceptual constraints: a cause for deviations from an ideal free distribution. Behav Ecol Sociobiol 19:409–415

Courtney SP, Parker GA (1985) Mating behaviour of the blue tiger butterfly (*Tarucus theophrastus*): competitive mate-searching when not all females are captured. Behav Ecol Sociobiol 17:213–221

Davies NB, Halliday TR (1979) Competitive mate searching in common toads *Bufo bufo*. Anim Behav 27:1253–1267

Fretwell SD, Lucas HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36

Godin J-GJ, Keenleyside MHA (1984) Foraging on patchily-distributed prey by a cichlid fish (Teleostei: Cichlidae): a test of the ideal free distribution theory. Anim Behav 32:120–131

Harper DGC (1982) Competitive foraging in mallards: 'ideal free' ducks. Anim Behav 30:575–584

Lester N (1984) The feed: feed decision: how goldfish solve the patch depletion problem. Behaviour 89:175–199

Milinski M (1979) An evolutionary stable feeding strategy in sticklebacks. Z Tierpsychol 51:36–40

Milinski M (1984) Competitive resource sharing: an experimental test of a learning rule for ESS's. Anim Behav 32:233–242

Milinski M (1986) A review of competitive resource sharing under constraints in sticklebacks. J Fish Biol [Am] 29:1–14

Parker GA (1970) The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoria* L (Diptera: Scatophagidae). II. The fertilisation rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. J Anim Ecol 39:205–228

Parker GA (1974) The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoria* L (Diptera: Scatophagidae) IX. Spatial distribution of fertilisation rates and evolution of male search strategy within the reproductive area. Evolution 28:93–108

Parker GA, Sutherland WJ (1986) Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Anim Behav 34:1222–1242

Shingler JJ (1985) Ideal free searching by cichlid fish. BSc Thesis, University of Liverpool

Sutherland WJ, Parker GA (1985) Distribution of unequal competitors. In: Sibly RM, Smith RH (eds) Behavioural Ecology: Ecological Consequences of Adaptive Behaviour. Blackwells, Oxford, pp 225–274

Thornhill R (1980) Sexual selection within mating swarms of the lovebug, *Plecia nearetica* (Diptera: Bibionidae). Anim Behav 28:405–412

Whitham TG (1980) The theory of habitat selection: examined and extended using *Pemphigus* aphids. Am Nat 115:449–466