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Relative competitive success of unequal competitors changes with overall density

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A group of 10 individually identifiable cichlid fish were used in a two-patch continuous input situation to examine the effect of density on relative competitive success of unequal competitors. Sutherland and Parker have proposed that relative intakes of unequal competitors can either remain constant across densities or that at higher densities better competitors will achieve higher gain rates. They also suggest that past continuous input situations have tended to fit the former prediction. We examined the influence of competitive ability on intake at different densities resulting from movement of fish between the two patches. This showed that contrary to the predictions of any model, in our system the best competitor did better relative to other individuals at lower densities, whereas the poorest competitor did better at higher densities. Fish of intermediate ability showed an intermediate effect of density on intake. As density increased there was a decrease in the difference between individual intakes, rather than the increase predicted by Sutherland and Parker's model. We suggest that this finding may be the result of competition switching from a contest between individuals at low density to a scramble for resources at higher density.

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The question of where and when animals choose to forage is one of the most significant challenges facing behavioural ecology. Most theoretical work on optimal patch choice has been based on the concept of the 'ideal free distribution' (IFD) (Brown 1969, Orians 1969, Fretwell and Lucas 1970, Parker 1970, 1974). Simple IFD models predict that if the environment is composed of resource patches of varying quality, then newly colonising animals will prefer to forage in the highest quality patches. However, as their density on these patches increases, their intake decreases due to competition, and previously inferior patches become equally profitable. If animals are of equal competitive ability then this process leads to an equilibrium at which intake rates are identical for all competitors on all patches.

Subsequent empirical investigations into competitive distributions have revealed that foragers rarely have equal competitive abilities, violating a key assumption of simple IFD theory (see Parker and Sutherland 1986). This has led to the development of models which take into account differences in competitor phenotype (Sutherland and Parker 1985, 1992, Parker and Sutherland 1986, Korona 1989). Sutherland and Parker's models describe two alternative ways in which the relative intakes of phenotypes differing in ability may vary with density. In the 'phenotype scales slope' model, phenotype affects the gradient of a graph of log (intake rate) against log (competitor density). Therefore, as density increases, superior competitors do proportionally better than inferior competitors.

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Alternatively, in the 'phenotype scales intercept' model, only the intercept of the log (intake) against log (density) graph differs between phenotypes. Hence, in this model, the relative success of different phenotypes is constant across densities. Sutherland and Parker (1992) suggest that past studies of continuous input situations tend to fit the predictions of the intercept scaling model. However, we know of no studies in which anyone has attempted to test experimentally whether density affects the relative intake rates of competitors in the ways predicted by the models (see Tregenza 1995a for a review of empirical work). In this study we use a continuous input resource system and different densities of individually recognizable competitors to investigate for the first time this essential assumption of contemporary ideal free theory. In doing so, we also illustrate a problem inherent in testing models that predict changes in the relative success of competitors with density; namely, that it is impossible to measure competitive ability directly without doing so at particular densities.

Methods

A group of 12 cichlid fish, *Aequidens portalegrensis*, were housed in a glass tank 60 cm long, 30 cm wide and 45 cm high and maintained at a temperature of 25°C by an internal heater/thermostat. At each end, water was pumped out of the tank by an internal power filter and returned through a funnel used as the food delivery system. Items of food dropped into the funnels entered the tank at sufficient speed to prevent one fish from monopolizing the resource. The bottom of the tank was kept bare to ensure that food could not accumulate.

The fish were monitored using a Sony Hi8 video camera mounted in front of one half of the tank which was lit from above. To minimise disturbance to the fish and reflections on the glass, blinds were fitted around the tank so that it could only be viewed through the camera.

The fish were fed items of '*Aquarian*' flake food (PO Box 67, Elland, W. Yorks) of a single type, standardised for size to between 5 mm and 7 mm diameter by sieving. Flake food was used because its large surface area : volume ratio meant that each item was easy to identify on the video recording. The experimenter dropped items of food into the funnel at set intervals. Two experimental runs were conducted each day. To minimize variance among males in motivation due to hunger, the fish were fed between runs by sprinkling food onto the surface of the water. The duration of each run (10 min) was chosen since it was sufficiently short to avoid any fish becoming satiated.

Fish were marked by injecting Alcian Blue dye under the scales using a modified (low power) 'Panjet' needleless injector system, (Wright Dental Co., Kingsway West, Dundee). This type of marking (described by Patterson (1985)) does not harm the fish or impair their competitive behaviour. Fish were not anaesthetized since the potential for suffering as a result of anaesthetization was judged to be greater than for marking without anaesthetic. Within a few minutes of being marked, fish displayed normal behaviours such as feeding and interacting with other fish and showed no signs of distress. Marks were placed on different areas of the body and used in conjunction with natural polymorphisms to allow individual recognition.

The fish aggregated around the funnel outlet where food items dropped into the water column. Using 1/24th of a second frame by frame advance, slow motion and multiple playback of the video recording it was possible to identify which fish had gained each item of food.

Determining relative competitive abilities

In order to determine the fishes' relative competitive abilities, we conducted a series of experiments which involved feeding the group of 12 fish from one end of the tank only. An item of food was washed into the tank via the funnel every 5 s for 10 min. The fish which gained each item was recorded. Twenty-six trials were conducted and the mean gain rates for each fish used to construct a rank order of success in acquiring food items.

Examining the influence of density on relative competitive success

Before the main experiment, the lowest ranking pair of fish were removed from the experiment, since they did not appear to be completely healthy. Food was input to both ends of the tank simultaneously. One end received 1 item every 5 s whilst the other received 1 item every 10 s. Only the end of the tank receiving an item every 5 s was recorded. The end of the tank receiving the high or low input rate was kept constant in order to give the fish a chance to learn the resource distribution. Forty experimental runs, each lasting 10 min were conducted. Analysis of the video tape revealed which fish gained a food item and the location of individuals during each 10-s period. The assumption that the ends are patches seems reasonable, since fish tended to concentrate their attention on one feeder at a time, and did not drift between the two. Therefore, those fish present at the observed end during each 10 s can probably be assumed to be taking part in competition for food on that patch.

Results

The initial experiment to determine the relative competitive success of individuals revealed that fish differed

Table 1. Estimated slopes from separate logistic regressions of feeding success on competitor density for each individual illustrate the varying effect of density on food intake for individuals of differing competitive ability. Significant negative slopes, representing a decreased probability of gaining a food item at greater density, are restricted to the top half of the hierarchy, while poorer competitors were either unaffected by density or increased their feeding success at higher density (poorest competitor). A multivariate logistic model considers all 10 relationships simultaneously and confirms the significant interaction between density and relative competitive ability in determining feeding success (see Results). Results in bold type are those fish which showed a statistically significant change in their probability of gaining a food item with density, as determined from log-likelihood ratio (*G*) tests.

Rank	Mean ± SE percentage intake[a]	Slope of regression	*n* (feeding opportunities)	*G*	*P*
1	**16.5** ± 0.7	**−0.379**	**948**	**110.8**	**<0.0001**
2	16.2 ± 1.3	−0.003	479	1.26	>0.50
3	**14.8** ± 1.1	**−0.099**	**856**	**7.21**	**<0.01**
4.5	**11.6** ± 1.1	**−0.211**	**541**	**7.83**	**<0.01**
4.5	**11.6** ± 0.8	**−0.103**	**771**	**4.92**	**<0.05**
6	10.7 ± 0.8	−0.249	23	0.79	>0.25
7	8.5 ± 0.6	−0.014	664	0.07	>0.75
8	5.3 ± 0.8	−0.042	740	0.54	>0.25
9	3.5 ± 0.6	−0.067	401	0.43	>0.50
10	**0.7 ± 0.2**	+0.271	**689**	**4.71**	**<0.05**

[a] Competitive ranks and percentage intakes determined from prior observations of all 10 fish feeding in one group.

consistently in the proportion of food items they acquired when feeding in a group. For the 10 fish used in the subsequent variable density experiment, the mean percentage of food items taken by each fish over all 26 trials differed significantly among individuals (ANOVA on arcsine-transformed percentage intakes $F_{9,250} = 62.28$, (factor df = 10 − 1 fish, residual df = (260 − 9 − 1) observations), $p < 0.0001$), and were consequently used to ordinally rank individuals by relative competitive success (Table 1). For a majority of the 10 fish, relative competitive success, or rank, did not change across the 26 trials; the relative number of food items taken each by the most successful competitor and the five least successful competitors did not vary significantly across the 26 trials (heterogeneity $\chi^2 = 86.83$, df = 6 fish across 26 trials = (6 − 1) × (2 − 1) = 125, $p > 0.5$). However, fish of relatively high competitive ability, or those ranked 2–5 in the hierarchy of overall feeding success, varied substantially across trials in their success at acquiring food (heterogeneity $\chi^2 = 266.46$, df = 4 fish across 26 trials = (4 − 1) × (26 − 1) = 75, $p < 0.0001$). Within this subset of good competitors, relative success fluctuated, making the allocation of overall ranks imprecise (Table 1).

Because the fish in these experiments can go to one of two feeding stations, the density at a given station varies as the fish move around. This makes it possible to examine the feeding success of differently ranked fish at different densities. We believe pseudoreplication is not a significant problem for this experiment since each item of food entering the tank represents a discrete opportunity for competition to occur. Furthermore, fish frequently moved between ends of the tank so that consecutive measurements would rarely have been made on the same group of fish. For instance, when only three fish were present, they would not have been the same individuals in each case. Using a limited number of fish could be described as pseudoreplication, although the fact that group composition varied argues against this. Numerous past studies have used the same fish repeatedly, (e.g. van Duren and Glass 1992, Croy and Hughes 1991, Godin and Keenleyside 1984, Sutherland et al. 1988), and as in these studies, we are assuming that the behaviour of a particular group of fish is not atypical.

An individual fish competing for food can either gain a whole food item or none at all. Because of these discrete outcomes, we used a logistic regression model to determine the effects of density and relative competitive ability on an individual's probability of gaining a food item. The mean percentage of food items gained by an individual across the 26 trials of the preceding experiment (Table 1) served as our measure of relative competitive ability since ordinal ranks did not reflect true differences in competitive ability with sufficient accuracy. Parameters in the logistic regression model have been estimated with a maximum likelihood procedure and tested for statistical significance with log-likelihood ratio (*G*) tests (Sokal and Rohlf 1995).

The full logistic model including competitor density and relative competitive ability explained a significant portion of the uncertainty in individual feeding success ($n = 6123$ per capita feeding opportunities, $R^2 = 0.10$, $G = 728.81$, df = 1, $p < 0.0001$). Since more fish competed for food items at higher density, it is not surprising that the probability of gaining a food item generally decreased with density (model coefficient = −0.20, $G = 14.87$, df = 1, $p < 0.0001$). Similarly, individuals previously shown to be better competitors for food items were more likely than competitors of relatively lower ability to gain a food item (model coeff. = −0.34, $G = 134.84$, df = 1, $p < 0.0001$). Of greater interest to us is the significant change in the influence of density on the probability of feeding success as competitors of different abilities were compared, i.e. the statistical interaction between density and relative competitive ability in their effects on gaining a food item (model coeff. = 0.03, $G = 54.73$, df = 1, $p < 0.0001$). As density increased, the probability of gaining a food item decreased significantly for all but one of the top five competitors, and it decreased most strongly for the highest ranked competitor (Table 1). In contrast, changes in density had no detectable effect on lower ranking competitors, except for the worst competitor, which actually increased its probability of gaining a food item at higher density.

Discussion

Current ideal free distribution theory considers two ways in which density may influence the relative success of individuals. Relative intake rates may be predicted to remain constant at different densities, so that regardless of patch, a forager which has twice the competitive weight of another will always gain twice as much food as that individual (Sutherland and Parker 1985, 1992, Korona 1989). Alternatively, better competitors are predicted to achieve relatively higher intake rates at higher densities (Sutherland and Parker 1992), so there is no constant relationship between the intakes of individuals. This is not a trivial difference since if better phenotypes do better at high density ('phenotype scales slope') they will go to high-value patches where there are more competitors, leaving poor patches containing poor competitors. This creates a 'truncated distribution' of competitor phenotypes (Parker and Sutherland 1986) in which patch quality is correlated with competitive ability. Any individual which switches to a better or poorer patch will decrease its intake. The only exception being individuals of a competitive weight intermediate between the mean for two patches adjacent in the rank order of patch types. Such 'boundary phenotypes' will be able to mix across two patches of different quality and achieve equal gains on each. In contrast, if density does not affect relative success, the intercept scaling model predicts a range of equilibria in which different combinations of competitor phenotypes may occur on the patches. The equilibrium depends on the starting conditions and there is no predictable relationship between phenotype and patch quality. Korona (1989) also assumes no change in competitive ability between patches. However, his 'local competition' model predicts that there will be a unique equilibrium at which each phenotype occurs in the same proportion in each habitat.

Sutherland and Parker (1992) suggest that changes in relative intake with density may be more likely in situations where intake is limited by search time as well as interference, whereas continuous input situations, where exploitation competition is dominant may tend to conform to the 'phenotype scales intercept' model.

In this study we found that relative payoffs did vary with density. However, contrary to the assumptions of the 'phenotype scales slope' model, our results suggest that better competitors may be more adversely affected by increased density than poor competitors. The best fish showed the strongest change in intake with density, and the biggest decrease in intake. Conversely, the poorest competitor actually increased its probability of gaining a food item as density increased, despite the greater number of fish competing for each item. Those mid-ranked fish in which a significant effect of density could be detected showed an effect of density on intake between the two extremes. It is important to note that these conclusions are based upon our initial ranking of individuals, measured at the maximum density. It can be seen from the slopes in Table 1 that density changes can also lead to changes in the rank order of individuals. For instance, the most successful fish (ranked 1) at maximum density is less successful than the 2nd ranked fish at lowest density. This is a problem inherent to testing competition models using real measures of ability, rather than surrogates such as size which may or may not give an indication of ability. Nevertheless, it is apparent that despite the arbitrary nature of creating a rank order of competitors at a particular density, in our study, although relative intakes change with density, the overall ranks change very little. Therefore, relative competitive success is still meaningful and consistent regardless of density, whereas probability of getting a food item is affected by both relative ability and density, but not in the way assumed by the model. It is possible that the reason for the lack of fit to the assumptions of the model is that the mechanism of competition changes as the density changes. At low densities better competitors may be able to harass other fish, whereas, as density increases, competition may switch from this 'contest' type to a simple scramble for resources. When there are very few fish, the best competitor may be able to partially monopolise the food input site, preventing the poorest competitors from feeding. At higher densities, competitor pressure prevents monopolization and the poorest competitors may be more able to get near to the input point. We were unable to quantify any such effect in this study, and previous work (Tregenza 1995b) using a simple measure of agonistic behaviour, namely the number of attacks fish make on each other did not reveal any variation with density. However, further work in this area would be valuable.

This study indicates that density may have even more potential effects on relative intake of unequal competitors than those already suggested by theorists. IFD models which assume constant relative payoffs such as the 'phenotype scales intercept' and Korona's 'local competition' model and Sutherland and Parker's intercept scaling model will clearly not be applicable to some foraging situations which on the surface would appear to conform to the models' assumptions. Further investigations into how competitors affect each other's intakes would be very valuable.

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