

# Unequal competitor ideal free distribution in fish?

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## Summary

Key predictions of unequal competitor ideal free distribution models were tested using a continuous input situation. Ten individually identifiable cichlid fish competed for food items at either end of their tank. Their distribution fitted the predictions of the equal competitor, continuous input ideal free model almost perfectly. However, examination of individual intakes revealed significant variation in individual success and relative competitive ability between patches. Contrary to expectations, fish did not exclusively use the patch where their intake was higher, although individuals experiencing greater differences in intake rate between patches were more selective. We found no evidence for a truncated distribution or even a correlation between competitive ability and patch quality. Changing the input regime to reduce competition did not produce a decrease in the range of intake rates between individuals. This study indicates the value of future empirical and theoretical work on how relative competitive ability varies with the nature of the foraging environment.

*Keywords:* *Aequidens portalegrensis*; competition; continuous input; ideal free distribution; patch choice

## Introduction

The way in which animals are distributed around their environment is central to our understanding of their ecology. The appropriate approach to the question of distribution depends on the size of resource patches relative to the ability of consumers to move between them. If resource patches are considerably larger than the home range size of animals, then we expect population dynamics to produce an equilibrium between resource population densities and consumer population density (see Rosenzweig, 1977). Alternatively, if consumers can choose between a number of resource patches, their distribution will result from individual decisions. In this paper, we concentrate on the latter scenario, and describe an experiment designed to indicate which aspects of individual behaviour we need to investigate to increase our understanding of competitive distributions.

Both closed patch models and those in which individuals move between patches predict equalization of fitness across habitats. In the former, this is achieved through long-term effects on local dynamics of high numbers (depletion, interference or both), whereas in the latter, the same equalization can be achieved much more quickly. The study of this second type of system has been dominated by the concept of the 'ideal free distribution' (IFD) (Fretwell and Lucas, 1970; see also Brown, 1969; Orians, 1969; Parker, 1970, 1974). The basis of the IFD is the idea that, as competitor density on a patch increases, its 'suitability' decreases. Individuals move to patches of high suitability, and in doing so create an equilibrium at which patches of different intrinsic quality prove equally suitable. This equilibrium is the 'ideal free distribution'.

Fretwell originally formulated the IFD in terms of large habitat patches with an emphasis on stasis rather than on continual patch hopping. In contrast, Parker's description (at around the same time) of an 'equilibrium position' where male mating success is equalized across patches

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differing in the rate of female arrivals, was inspired by his study of dungflies, which continually move between cowpats. It remains a striking feature of ideal free models that they have proved applicable both to systems with very small-scale patchiness and rapid patch movements (such as dungflies) and to systems where habitat choice is almost a once-in-a-lifetime decision (such as in catfish choosing between pools; Power, 1984).

At the same time as his proposal for an IFD, Fretwell suggested an alternative scenario, where individuals defend resources to the exclusion of competitors. This creates a distribution in which equalization of fitness across habitats is prevented by territoriality, a situation he termed the 'ideal despotic distribution' (Fretwell, 1972).

In the development of IFD theory, the assumption made by early models, that competitors have equal abilities, has been replaced by more realistic scenarios in which differences in competitor phenotype are taken into account (Sutherland and Parker, 1985, 1992; Parker and Sutherland, 1986; Korona, 1989; Holmgren, 1995). However, these models vary in their applicability. Sutherland and Parker suggest two alternative approaches to competitive differences. Better competitors either simply gain proportionally more resources than poorer competitors regardless of the habitat, or they are able to capitalize on their superior abilities to a greater extent in higher quality patches. Holmgren's unequal competitor IFD based on a functional response is specifically formulated for a situation in which resource items are distributed around a patch, and interference takes the form of kleptoparasitism. In this situation, search and handling time limit intake. Korona's model, based on one-on-one contests, assumes that the food in a patch is simply divided up among competitors, with no other influence on intake.

The differences between the models mean that as approaches to apparently similar problems, they are not alternatives, but rather address different foraging scenarios. To some extent, this divergence is an inevitable consequence of attempts to describe distributions more accurately. As models become more specific, they gain descriptive power, but lose generality, since fewer foraging situations conform to their assumptions. To improve our understanding of competitive distributions, we need to identify which aspects of current theory can be modified to increase predictive power without excessive reduction of generality.

All the models have in common that to test their predictions we must first gain some measure of the relative competitive abilities of our study animals. This must be done in advance of distribution experiments to avoid defining competitive weights according to the predictions of the theory and hence creating a circular argument. This raises a problem inherent in such models, in that any attempt to quantify competitive ability precisely can only do so using one particular foraging scenario in terms of number of competitors and patches. This difficulty has generally not been addressed by empiricists, who have tended to measure relative competitive ability at one density only, typically all competitors foraging on a single patch (e.g. Sutherland *et al.*, 1988; Inman, 1990; Croy and Hughes, 1991; Grand, 1997). This is likely to provide a more relevant measure than rankings based on aggressive interactions between pairs of individuals (e.g. Järvi and Pettersen, 1991), and it allows more precision than the alternative of using a surrogate for competitive ability, such as size or maturity (e.g. Milinski *et al.*, 1995). Theoretically, it would be possible to take each individual and observe its success in competition with a standard group of conspecifics. However, the problems associated with introducing a strange individual to an established group make it likely that this would create more problems than it would solve. If we use the mean percentage intake over the entire experiment as a measure of competitive weight to make it more representative, then a circular definition of the term becomes inevitable. Overall, it seems that constructing a ranking from observation of all individuals foraging together on a single patch may be the best option, although studies of variation in competitive abilities according to the nature of the foraging situation will be valuable (see Tregenza *et al.*, 1996b).

In this paper, we test the predictions of two unequal competitor IFD models – those of Parker and Sutherland (1986) and Sutherland and Parker (1985, 1992) – and Korona's (1989) model. Both models address a situation in which competition is the result of sharing resources that arrive continuously in a patch. This type of 'continuous input' situation is attractive to theoreticians because input regime and competitor density are the only factors influencing intake rate. Because resource items arrive on the patch at a lower rate than the maximum consumption rate, factors such as search time and handling time can be ignored. However, this tractability is bought at the cost of lack of similarity between foraging scenarios used to develop models and the real world. Many foraging situations cannot be described by continuous input models and, in the real world, the highly clumped, highly patchy resources assumed by continuous input models may tend to be associated with despotism. On the other hand, if an IFD is observed even in experimental systems with point sources of food, the implication must be that such distributions should be very common in nature where resources tend to be more diffuse.

It has recently been shown that, even if we relax the assumption that items are consumed as soon as they enter a resource patch, the models' predictions remain robust (Lessells, 1995; Tregenza *et al.*, 1996a). Furthermore, a number of field studies have indicated that continuous input may be a suitable approximation of the foraging environment of grazing fish (Power, 1984), fishermen (Abrahams and Healey, 1990; Gillis *et al.*, 1993), dungflies (Parker, 1970, 1978), lovebugs (Thornhill, 1980) and lekking birds (Alatalo *et al.*, 1992).

Using a continuous input system conforming to the basic assumptions of these models, we aimed to test five key predictions:

1. If there are differences in intake rate between patches, animals will go to the patch where their intake rate is highest.
2. The distribution of unequal competitors leads to an equal intake rate per competitive weight unit across patches. Competitive weight is a measure of the relative competitive ability of individuals. An individual with twice the competitive weight of another on a particular patch should have twice the intake rate. Even if competitive ability cannot be measured independent of the foraging situation, we can still examine a less specific prediction of unequal competitor models, which is that the mean rank of fish should be inversely correlated with the number of fish in a patch (Sutherland *et al.*, 1988).
3. Sutherland and Parker's (1992) 'interference' model predicts that, if relative intake rates vary across patches, there should be a truncated distribution with better competitors occurring exclusively in the higher input patches and poorer ones in the lower input patches. In contrast, their 'continuous input' model and Korona's (1989) model predict that a range of phenotypes will occur in all patches.
4. A less demanding prediction of Sutherland and Parker's (1992) unequal competitor interference IFD model is that competitive rank should be correlated with percentage of time spent in the better site.
5. If the food regime is changed so as to give less advantage to better competitors, this should lead to a reduction in the range of intake rates between individuals.

## Methods

### *Choice of experimental animal*

We are not seeking to investigate habitat selection in fish *per se* (see Kramer *et al.*, 1996). Our aim is to use captive fish as a model system from which conclusions relevant to other groups can be

drawn. We are concerned with the natural feeding ecology of our fish primarily in that it must be sufficiently similar to our experimental set-up to have a reasonable expectation that the behavioural rules necessary for IFD will have evolved. For this reason, and for the reasons set out below, we chose to use juveniles of a cichlid fish, *Aequidens portalegrensis*:

1. Although now uncommon in their natural habitat in south-eastern Brazil, they previously occurred at high densities. Their shallow stream environment includes patchy food resources and intraspecific competition, making it likely that they evolved the learning rules necessary for ideal free distribution. Any subsequent adaptation to aquaria will have reinforced this behaviour, since food supplied to aquarium fish tends to be extremely clumped in both space and time.
2. They compete vigorously for food. Many animals are poorly suited to IFD studies where patch quality is assumed to depend on resources, since their fitness is strongly dependent on factors other than resource competition. They are still expected to conform to an IFD, but one that must take into account factors that are difficult to manipulate.
3. They are non-territorial when juvenile, avoiding violation of the assumption that all animals are free to enter any patch.
4. They are able to move rapidly between feeding stations at either end of the tank without wasting much time or energy, allowing travel costs to be ignored.
5. They are relatively easy to observe using appropriate equipment, since their distribution can be observed 'side on'. Using fish marked with spots of dye injected under the scales, it is possible to identify individuals, allowing assessment of individual success.

#### *Experimental apparatus and procedure*

A group of 12 fish was housed in a glass tank (120 × 30 × 45 cm) maintained at a temperature of 25°C. At each end, water was pumped out of the tank and returned through a funnel, which was used as the food delivery system. Items of food dropped into the funnels were carried in the water flow into the tank sufficiently fast to prevent one fish from monopolizing the resource.

The fish were monitored using a Sony Hi8 video camera mounted in front of either half of the tank, which was lit from above. Two square cone blinds were fitted side by side in front of the tank. The camera fitted into the small end of the cone, with the large end covering the front of the tank. This eliminated reflections from the front of the tank and prevented the fish from being disturbed by movement outside the tank.

The fish were fed items of flake food of a single type, standardized for size to between 5 and 7 mm diameter by sieving. We used flake food because it is only slightly negatively buoyant and 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. The food regime was varied either by changing the frequency of food items input or by changing the number of items of food simultaneously placed into the funnel. Two experimental runs were conducted each day. Between runs, the fish were fed by sprinkling food onto the surface of the water.

Fish were marked by injecting Alcian Blue dye under the scales using a modified (low-power) 'Panjet' needle-less 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 anaesthesia 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 variation to allow individual recognition.

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

To measure individual competitive abilities, it is necessary to use the same group of fish in consecutive trials. Therefore, as in other ideal free experiments in which individuals have been used repeatedly (e.g. Harper, 1982; Godin and Keenleyside, 1984; Sutherland *et al.*, 1988; Croy and Hughes, 1991; van Duren and Glass, 1992), we assumed that the behaviour of a single group is likely to provide some insight into the behaviour of other groups. Furthermore, continuous input experiments inevitably produce a situation in which data points cannot be considered strictly independent, since if one fish gains a particular item of food, no other fish can consume it. This has tended to be ignored in past unequal competitor studies in which analysis of variance has been used to compare individual intakes (e.g. Godin and Keenleyside, 1984; Sutherland *et al.*, 1988; Grand, 1997). We attempted to minimize the dependence of our data points by using a larger number of fish (10 as opposed to 6, 6 and 8 fish, respectively, in the three studies mentioned above). Also, we analysed individuals separately, using multiple *t*-tests, with adjustment for increased likelihood of a type 1 error (sequential Bonferroni method; Holm, 1979).

#### *Determining relative competitive abilities*

To determine the fishes' relative competitive abilities, we conducted a series of experiments 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 and the fish which gained each item was recorded. Twenty-five replicates were conducted and the mean intake rates for each fish used to construct a rank order of success in acquiring food items. The percentage of available resources gained was used to determine the relative abilities of the fish, equivalent to Sutherland and Parker's (1985) competitive weights. Following the determination of competitive weights, the two lowest ranking competitors were removed, since their intake was so low that it was considered that their distribution was unlikely to be dictated by their intake rates during experiments.

#### *Unequal competitor IFD*

Food was input to both ends of the tank simultaneously. One end received one item every 5 s, while the other received one item every 10 s. Because it was impossible to record both ends of the tank simultaneously while achieving the resolution required for individual recognition, the observed end was alternated between runs. After each 10 min run, the videotape was analysed, noting the fish gaining food and the presence or absence of each individual during each 10 s period. Because each half of the tank was classified as a food patch, the distribution across both patches could be inferred from the fish occurring at one end. Fish were very rarely observed moving between patches more than once in any 10 s period, allowing us to measure rates of patch switching using the residence data (Fig. 1). The assumption that the ends are patches seems reasonable, since items of food were typically consumed less than 1 s after input (see Tregenza *et al.*, 1996a), so fish were unable to forage at both ends simultaneously in both patches.

#### *The effect of reducing competition*

To test the prediction that a reduction in the opportunity for competitive ability to manifest itself will lead to a contraction in the range of intake rates, we changed the feeding regime. Instead of adding one item every 5 s to the high-quality patch, we added four items together every 20 s. This does not change relative patch qualities, but means that better competitors can take only a max-

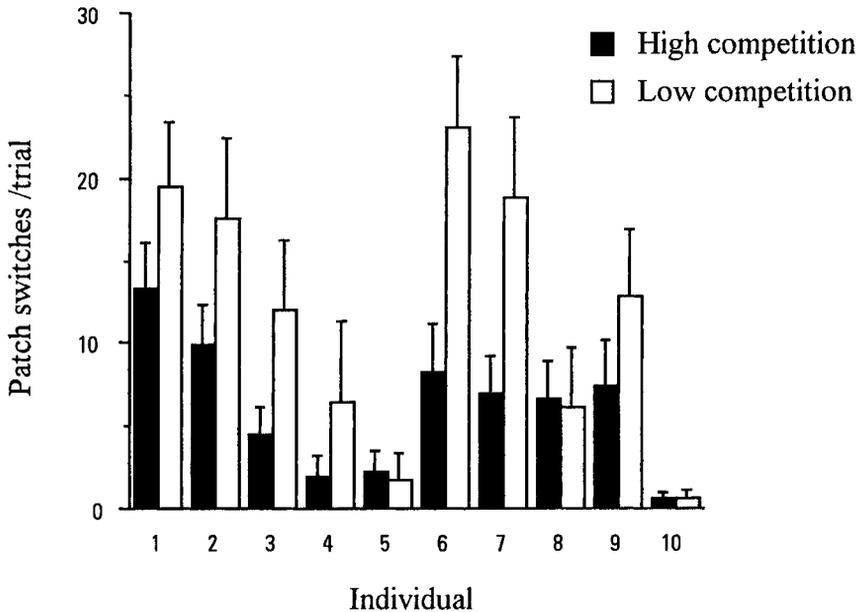


Figure 1. Number of patch switches made by each individual with food items entering the tank one at a time at each end (high competition) and with five items entering simultaneously (low competition). Bars are 95% confidence limits.

imum of one item in four, since the differences between competitors were not large enough to allow better competitors to take more than one item of food if all items entered together (except on rare occasions).

## Results

### *Do competitive abilities remain constant?*

It is apparent from Table 1 that, although there were significant differences between individuals in the ranking experiment (ANOVA:  $F_{11,288} = 62.28$ ,  $P < 0.0001$ ), the rank order of competitive success changed considerably between experiments and ranks were not significantly correlated between the competitive ability experiment and the subsequent experiment (Spearman's rank correlation coefficient:  $r_s = 0.53$ ,  $P = 0.117$ ). This indicates that competitive abilities changed with time or with the exact nature of the foraging situation. It is apparent that changing the food regime affects behaviour, since the rate of patch switching increased for all but one competitor when the food input regime was changed from one item every 5 s in the good patch to four items simultaneously every 20 s (Fig. 1).

### *Is there equal intake per competitive weight unit across patches?*

Because competitive ability cannot be measured independent of the foraging situation, it is impossible to determine whether there was an ideal free distribution of competitive weights. However, we can still examine the less specific prediction that the mean rank of fish should be correlated inversely with the number of fish in a patch. Using either the rank order determined in the initial

Table 1. Competitive weights and rank order of fish in initial relative competitive ability trial and subsequent IFD experiments. Initial rankings are used to refer to individuals throughout the paper

Fish numbered by rank in competitive ability experiment	Mean percentage intake			New rankings	
	Competitive ability experiment ( <i>n</i> = 25)	High competition (1/5 s + 1/10 s) ( <i>n</i> = 40)	Low competition (4/20 s + 1/10 s) ( <i>n</i> = 14)	High competition	Low competition
1	17.96	24.78	23.19	1	1
2	17.96	10.94	9.55	3	5
3	15.96	10.73	13.80	4	3
4	12.39	7.61	12.12	7	4
5	12.00	8.26	1.56	6	10
6	11.96	2.57	7.19	10	6
7	9.35	14.09	14.15	2	2
8	6.08	6.41	6.07	8	8
9	3.96	5.65	6.05	9	9
10	0.77	8.97	6.32	5	7
11	0.54	removed			
12	0.04	removed			

experiment, or a rank order determined from the gains achieved at densities of seven or more fish during the experiment itself, it is apparent that this prediction is corroborated (correlation of mean rank and density, using each rank order, respectively:  $r = -0.876$ ,  $n = 9$ ,  $P < 0.001$ ;  $r = -0.894$ ,  $n = 9$ ,  $P < 0.001$ ).

There is no evidence for truncation of competitive weights between patches using either measure of rank, since all but one competitor fed on both patches (Table 2). Furthermore, neither those competitors showing high intake, nor those with high rank in the initial trial, were found in the higher input patch only.

The less demanding prediction of Sutherland and Parker's (1992) unequal competitor interference IFD model, that competitive rank should be correlated with percentage of time spent in the better site, can be tested using the mean time spent in the better patch in each experiment for each individual. This revealed a significant correlation between percentage time spent on the patch and rank, using either the estimate from the rank determining experiment or that determined from the main experiment itself ( $r = -0.443$ ,  $n = 200$ ,  $F = 48.24$ ,  $P < 0.0001$ ;  $r = -0.192$ ,  $n = 200$ ,  $F = 7.56$ ,  $P < 0.007$ , respectively).

#### *Do some individuals do better in one patch than in another?*

A repeated-measures ANOVA of transformed percentage intake rates (experiment means) against individual and patch shows that there were significant differences between individuals ( $F_{9,389} = 11.78$ ,  $P < 0.001$ ) and between their intake rates in different patches ( $F_{1,389} = 40.47$ ,  $P < 0.0001$ ). It can be seen in Table 2 that, in the case of 4 of the 10 fish, there were significant differences in the rate of intake between the two patches. Of these four, two did better in the lower input patch and two in the higher input patch. It is also apparent that relative competitive abilities varied across patches, since some individuals did better in the poorer patch and others in the good patch.

Table 2. Intake rate of fish in each of the two patches and the proportion of time spent in each patch<sup>a</sup>

Fish	Items gained/10 s in patch		% time spent in 1/5 s patch	% intake rate in both patches
	1/10 s	1/5 s		
1	0.00	0.74**	99	24.8
2	0.36	0.33	54	10.9
3	0.26	0.32	96	10.7
4	0.22	0.22	65	7.6
5	0.32**	0.14	43	8.3
6	0.13**	0.06	76	2.6
7	0.41	0.21	2	14.1
8	0.18	0.19	68	6.4
9	0.11	0.18	82	5.7
10	0.11	0.29**	85	9.0

<sup>a</sup> Asterisks indicate a significant difference between intake rates in the two patches at the Bonferroni-adjusted equivalent to 0.001 (see below). Using this method, despite having *t*-values which would normally indicate a significant result, we cannot consider the intakes of fish 7 and 9 to be significantly different between patches ( $P = 0.017$  and  $0.021$  respectively).

#### *Do fish choose the patch where their intake is highest?*

Simple intake maximization theory would predict that, if individuals experience higher intake on one patch, then they ought to spend all their time on that patch. Table 2 shows that, despite four fish showing significantly different intake rates between patches, they all continued to use the less favourable patch to some degree. However, only one actually spent the majority of its time on the patch where its intake was lower, and this was also the fish with the lowest foraging success of all individuals.

Table 2 also shows that individuals varied in the magnitude of the difference in their intake rates between patches. A correlation of the proportion of intake achieved on one of the patches against the proportion of time spent there, reveals that those individuals which experienced greater differences in intake rates between patches also showed stronger patch preferences (arcsine transformed proportions: first food regime (1/5 s, 1/10 s)  $r = 0.663$ ,  $n = 10$ ,  $P < 0.02$ ; second food regime (4/20 s, 1/10 s)  $r = 0.921$ ,  $n = 10$ ,  $P < 0.001$ ).

#### *Does adding several items of food simultaneously cause a reduction in variation in intake rates?*

If reduced competition leads to less advantage for better competitors, we would expect to see a reduction in the range of intakes from the best to the poorest competitors when several items are added together. This prediction should be robust even if competitive ability were changing over time. However, it is apparent from Fig. 2 that this was not the case in our study. Indeed, there is a suggestion that, except for the extremes, the lower competition scenario led to lower intake for poorer competitors and higher intake for better competitors, contrary to the theory. It is worth considering that the longer interval between additions of food could allow fish to 'shuttle' from one end of the tank to the other. However, although movement rates were higher under the reduced competition regime, a *t*-test of the number of fish in the good patch during the 10 s food input periods, as opposed to non-input periods ( $t_{429} = 0.97$ ,  $P = 0.33$ ), suggests that this behaviour was not occurring. Furthermore, the five fish which improved their intake following the change in regime did not break this pattern ( $t_{429} = 1.11$ ,  $P = 0.27$ ), being slightly less likely to be present on the good patch when food was input, than during non-input periods.

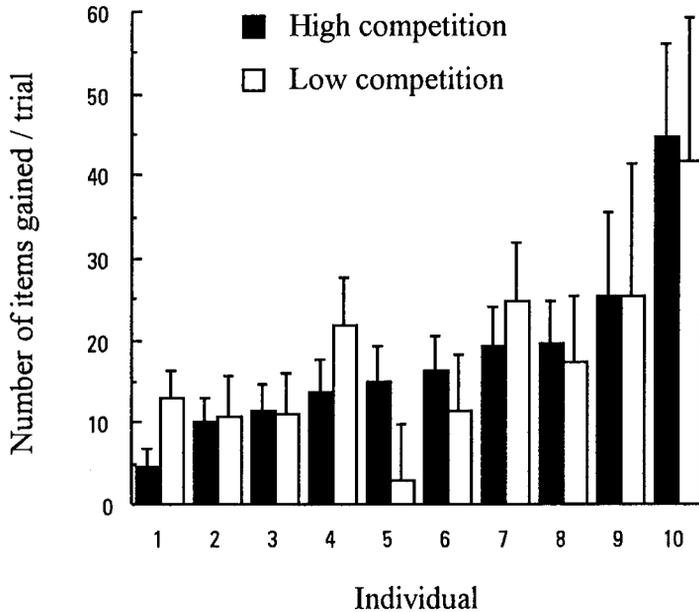


Figure 2. Individual intake per trial with food items entering the tank one at a time at each end (high competition) and with five items entering simultaneously (low competition). Bars are 95% confidence limits.

### Discussion

Our investigation of a competitive system revealed a number of interesting features, suggesting directions for future experimental and theoretical work. The finding that several individuals varied significantly in success and relative competitive ability between patches is contrary to the assumptions of Korona's (1989), Holmgren's (1995) and Sutherland and Parker's (1992) continuous input models. This lends support to models which do not make this assumption, such as Sutherland and Parker's (1992) 'interference' model. For the real world, this suggests that even apparently similar areas of the environment may prove more suitable for certain individuals than for others. Why this was the case in our system is unclear. There appeared to be a number of different strategies employed by fish to gain food, such as waiting directly below the input point and attempting to grab the food before it became available to all individuals, or darting in rapidly from further away. Also, although no fish prevented others from entering either patch, there were numerous aggressive interactions. It seems likely that the intake an individual can achieve is not only a function of input rate and the other individuals present, but also of the strategies being employed by those competitors.

Having established that there are differences in intake rate between patches, it is puzzling that fish nevertheless spend significant proportions of their time on the patch where their intake is lower and, in one case, even appear to prefer that patch. This is contrary to simple optimality theory, which predicts that animals should spend all their time on the patch where their intake is highest. Numerous past studies, in which competitors were considered equal, found a similar paradox, in that lower quality patches were overused, leading them to yield lower intake rates than better patches (see Tregenza, 1995). This has tended to be explained by invoking two different types of constraint. First, animals may be unable to distinguish between their intakes on different patches

when these are similar (Abrahams, 1986) and, secondly, they must sample their environment to determine patch qualities, and in doing so will be found in sub-optimal areas. In our system, either or both of these explanations may be relevant.

However, in our study, half those individuals with significant variation in intake rate did better on the lower input patch, a finding which is less consistent with previous work. A possible explanation for this result is that fish are trading off lower intake in the short term for decreased energy expenditure or exposure to aggression. Perhaps we are observing 'cryptic despotism', whereby individuals reduce competition in the patch they occupy not by excluding others, but by making it more costly for them to forage there. Such situations may prove difficult to make quantitative predictions about. The simplest scenario is equivalent to an ideal despotic distribution where despotic individuals are found on the best patch where they gain most from their behaviour. However, individuals vary in their ability to withstand despotic behaviour, so that some non-despots are nevertheless resistant to aggression; thus despots may not get everything their own way, and may find it more profitable to forage on a poorer patch. Perhaps despotism is best regarded as a continuum from complete physical exclusion, through attacking interlopers so severely that they invariably leave, to the type of situation observed in most continuous input IFD studies where there is aggression between individuals but no despotism in the conventional sense of the term.

An interesting feature of the level of apparent overuse of sub-optimal patches was the finding that, between individuals, increased differences in intake between patches led to increased patch selectivity. This is consistent with a perceptual constraints explanation for the use of inferior patches, since those animals which found patches more different would have less difficulty distinguishing where their intake was higher. Equally, this finding could be the result of sampling behaviour, since sampling will be less costly to an individual which experiences a lower decrease in intake when it leaves its optimal patch.

Another striking finding was that the relative competitive abilities of individuals varied with time and the foraging situation. The reasons for this variation are not obvious, but it is clear that, even within the strictures of continuous input resources, different scenarios can be produced which may affect different individuals in different ways. If there were a simple linear relationship between competitive ability and intake rate, then reducing competition by adding food items simultaneously would lead to a contraction in the range of intakes. Better competitors, no longer able to take full advantage of their abilities, would be expected to do worse, whereas poorer competitors would improve their intake. However, this was not the case in our system (Fig. 2), although there was a change in the relative success of individuals. It is possible that reducing competition by the simultaneous entry of food items allows competitors with particular abilities to increase their intake, but not others. For instance, being able to maintain a position near the input point might not confer great advantages when several items arrive at once, whereas an ability to move rapidly towards a food item might be more advantageous. Similarly, if we are dealing with cryptic despotism, more temporally clumped resources might benefit more aggressive individuals, or individuals able to withstand aggression for a short period. Whatever the case, our results suggest that this system is indeed more complex than the simplest scenario.

Our third aim was to determine whether this system fitted the predictions of Sutherland and Parker's (1992) 'interference' model, or their 'continuous input' model and Korona's individual contests model. As discussed earlier, relative payoffs to different competitors varied across patches, an assumption of Sutherland and Parker's (1992) 'interference' model, which is inconsistent with the other models. However, there is little evidence to suggest that there was a truncated distribution of competitor phenotypes. All but one competitor used both patches and, although the four highest ranked competitors spent more time in the good patch, so did the lowest ranked three. It is worth noting that, if this experiment is analysed ignoring the differences between individuals, as has been

done in numerous past studies, then the distribution appears to conform very closely to the IFD predictions. If the proportion of time each fish spends in each patch, as given in Table 2, is summed for all competitors equally, the ratio of individuals in the patches is 0.67 : 0.33, which is an exact fit to the prediction of the equal competitor input matching rule (Parker, 1978).

In general, this study has shown that even a relatively contrived system may prove too complex to allow predictions about distribution of unequal competitors using current theory. This system conforms exactly to the predictions of equal competitor IFD theory but, without the (unjustified) assumption of equality between individuals, fails to conform to the predictions of any model. To understand distributions in the real world, we will need to consider variation between individuals dependent on the nature of the environment in which competition occurs.

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