

An experimental investigation of a new ideal free distribution model

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Summary

We investigate a new continuous input ideal free distribution model which removes the assumption that resources are consumed as soon as they enter a patch. The model makes predictions about the standing crop of resources and allows consideration of the effects of simultaneous exploitation and interference competition. Using a group of cichlid fish competing for food items, we show that consistent with the model, standing crops can vary in continuous input situations. As predicted, higher standing crops are associated with increased intake rates. Furthermore, with greater numbers of competitors, standing crops are higher, suggesting that there is interference as well as exploitation competition in our system. An experiment to investigate the effects of fish density on the level of movement revealed that the reported interference competition could not be attributed to increased fish movement at higher density.

Keywords: *Aequidens portalegrensis*; competition; continuous input; exploitation; ideal free distribution; interference; standing crop

Introduction

Ideal free distribution theory (Fretwell and Lucas, 1970; Parker, 1970) provides the basis for a large body of theoretical and empirical work on the distribution of animals competing for resources (see Milinski and Parker, 1991; Tregenza, 1995a for a review). Numerous models assume that the presence of competitors decreases the profitability of a patch and that animals will go where their intake is highest and may do so without costs. Two distinct classes of model make predictions for two alternative forms of competition, exploitation and interference. Exploitation decreases intake rate due to a reduction in the density of resources present at any one time (the standing crop) causing increased search time. Interference decreases intake rate as a result of reversible, short-term effects of the presence of other foragers, such as time wasted in interactions. The majority of laboratory investigations into the IFD have been based on systems in which animals compete for food items which arrive one at a time in patches, where they are assumed to be consumed immediately. Parker (1982) predicted that these situations should conform to the 'input matching rule' such that the proportion of individuals found at any continuous input site should match the proportion of food input received by that site. Parker's model has been advanced considerably by Lessells (1995). Her continuous input model relaxes the assumption that resources are consumed immediately and makes a number of predictions about standing crops of resources and the effect of predator density and interference. In this paper we test the validity of some of these assumptions and predictions.

Lessells (1995) begins by assuming that resources are replenished at a constant rate and for the

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part of the model we wish to consider, only leave the patch when consumed. Animals are assumed to be of identical competitive ability. The individual consumption rate is a function of the standing crop of resources which is dictated by the input rate and exploitation. Variation in standing crops does not require that several resource items are present simultaneously; if a single item remains in the patch for a longer period, the standing crop is greater. At equilibrium, the per capita intake rate in all patches must be equal, so that in the absence of interference, the standing crop in all patches must also be equal. If interference occurs in addition to exploitation competition, consumers on patches with higher input rates and, hence, greater competitor density will waste more time in interactions with each other. Therefore higher input rate patches will have to have correspondingly higher standing crops in order to provide the same intake as lower input patches. This leads to standing crops increasing with competitor density across patches.

Since much past work on testing continuous input IFD models has been done using fish (e.g. Milinski, 1979, 1984; Godin and Keenleyside, 1984; Sutherland *et al.* 1988; Croy and Hughes, 1991, van Duren and Glass, 1992), we also used this system. We chose to use a cichlid fish, *Aequidens portalegrensis*, the brown acara, since cichlids are non-territorial when young and compete strongly for food. Lessells' (1995) model predicts the equilibrium distribution of competitors and standing crops when there is a choice of patches. However, we are able to test the key element of her theory, the mechanism by which stability occurs, using a system containing a single patch, since it can be considered to represent one patch in an equilibrium system. This is justified since numerous experiments using fish have shown that they are able to distribute themselves such that intake rates are equal across continuous input patches (see Milinski and Parker (1991) for a review). Furthermore, experiments on the species used here, in which a group of fish forage on two patches, one of which receives twice the input rate of the other, show that the mean intake per fish across patches is equal (Tregenza, 1995b).

During experiments, the fish were housed in a glass tank 60 cm long, 30 cm wide and 45 cm high, which was maintained at a temperature of 25°C by an internal heater/thermostat. Water was pumped out of the tank by an internal power filter and returned through a funnel at one end, which was used as the food delivery system. Items of food dropped into the funnel were carried in the water flow into the tank. The fish were monitored using a Hi8 video camera mounted in front of the tank which was lit from above. The fish were fed items of 'Aquarian' flake food (PO Box 67, Elland, W. Yorks) of a single type, standardized for size (diameter 8 mm \pm 1.5 mm) by sieving. Flake food was used since it is only slightly negatively buoyant and because its large surface area: eg volume ratio meant that each item was easy to identify on the video recording.

Seven densities (numbers of fish) were used: one, two, three, four, six, eight and ten. Before each experiment the fish to be used were selected at random from a group of 15 fish. Using the same fish more than once is less than ideal, since it could be construed as pseudo-replication. However, numerous past studies have used the same fish repeatedly (e.g. Godin and Keenleyside, 1984; Sutherland *et al.*, 1988; Croy and Hughes, 1991; van Duren and Glass, 1992) and as in these studies, we are assuming that the behaviour of a particular group of fish is not atypical. At each density the fish were fed for 2 min by dropping single items of food into the funnel, to which they responded immediately. Using multiple playback of the video recording, slow motion and 0.04 s frame by frame advance it was possible to measure how far each item of food dropped before it was eaten. We established that the standing crop was at equilibrium since linear regressions of drop distance against time yielded no significant patterns under any regime (maximum $F = 2.55$, $p = 0.113$). Plots of residuals did not indicate any curvilinear relationships. To determine whether fish moved more at higher density (which might result from interference), a grid of 5 cm squares was drawn onto the front of the tank. Movement was

Table 1. The effect of density on standing crops

| Density of fish | Mean drop distance (cm) | N^a | Number of food items entering patch per second | Standing crop ^b |
|-----------------|-------------------------|-------|--|----------------------------|
| 1 | 12.4 | 10 | 0.02 | 0.041 |
| 2 | 15.6 | 10 | 0.04 | 0.102 |
| 3 | 9.6 | 10 | 0.06 | 0.094 |
| 4 | 8.2 | 10 | 0.08 | 0.108 |
| 6 | 4.6 | 10 | 0.12 | 0.091 |
| 8 | 6.3 | 10 | 0.16 | 0.165 |
| 10 | 5.2 | 10 | 0.20 | 0.171 |

^aA single measure of standing crop was randomly chosen from each replicate.

^bMean number of items in water at a time.

assessed by counting through how many squares each fish moved during the 2 min period. Since the fish were over 5 cm long, the focal fish's right eye was used to determine which square it was in, (when facing the wrong way, it was possible to estimate the right eye's position using the left eye). At the higher densities, five randomly chosen fish were observed. Where the density was less than five, all fish were assessed. To examine the effect of competitor density on resource standing crops, the frequency of input was calculated for each density so that a constant ratio of food items per fish per minute was maintained across the densities (see Table 1 for details). Because all food items are consumed, there is a constant intake rate at all densities, as would be expected in an equilibrium system. To test the assumption that greater standing crops will lead to higher intakes, an identical set of experiments was performed using a constant input of one item every 5 s across all densities.

We established that it is possible to have differences in standing crops between patches, since there was significant variation in how far each item of food dropped through the tank before being consumed (drop distance) with density of fish (see Table 1) (one-way ANOVA $F = 9.12$, $df = 6,69$, $p = < 0.0001$). To avoid pseudo-replication, all analyses are performed using one instantaneous measure of standing crop selected at random from each experimental run. Drop distances were converted into standing crops using the mean of 50 5 cm drops, (again chosen at random, from ten separate runs of 20 items each) which were timed using the 0.04 s code recorded on the video tape (mean = 0.164 s cm^{-1} SE = 0.0082). In addition to consumption by the fish, standing crops can also vary if the input rate varies. However, the input rate is imposed by the experimenter, rather than being a dynamic feature of the system.

The second assumption we wished to test was that intake will increase with standing crop. By having the same food input rate to different densities of fish in the second set of experiments, we were able to manipulate the standing crop, so that it was higher at lower fish densities. Our results support the assumption, since (again using one instantaneous measure of standing crop from each experiment) higher standing crops were associated with higher intake (correlation of standing crop with intake $r = 0.43$, $n = 70$, $p = 0.0002$). Although this is intuitively obvious, since the intake rate is increasing with the input rate per fish, the relationship between the standing crop and the intake rate remained to be confirmed experimentally in a continuous input situation.

The confirmation that intake increases with standing crop allowed us to test the most interesting prediction of the model, that at higher density, standing crops should also be higher if there is interference. This prediction was also supported by our results (see Table 1). A regression of standing crop against density shows that as density increases, standing crops also increase ($r^2 = 0.21$, $F = 18.02$, $p = < 0.0001$, $n = 70$). The equilibrium standing crop is higher at

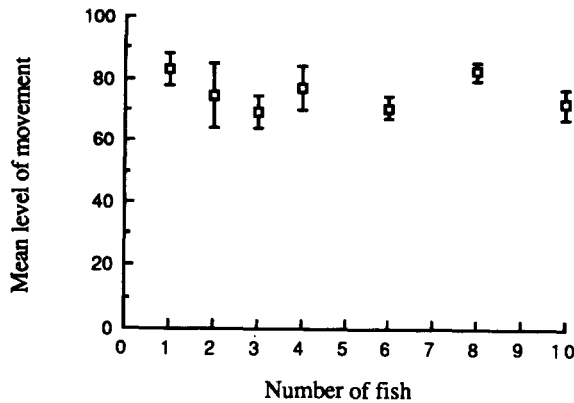


Figure 1. Variation in mean level of fish movement with density (bars are standard errors). Movement was measured as the number of squares the fish moved through over the period of observation. There is no detectable effect of density on the level of movement (one-way ANOVA on randomly selected fish from each experiment, $F = 0.79$, $df = 6,69$, $p = 0.58$).

higher density since more frequent food input is not balanced by more rapid consumption. It is worth considering that this effect might be an artefact of other aspects of the fish behaviour. For instance, if standing crop were to remain constant as the density increased, the fish would have to react faster to each item of food entering the tank. However, the fact that the mean distance continues to decline after several density increases, together with our observations of the fish, lead us to doubt that the change in standing crop results from the fish being unable to react faster.

In an attempt to investigate the source of interference, we measured the level of movement at each density. If greater numbers of competitors were leading to a requirement for fish to move around more, then this in itself would constitute an extra cost associated with higher density patches. However, our results suggest that the level of movement is relatively unaffected by changes in the density. It can be seen in Fig. 1 that an increase in density did not lead to higher levels of movement when the resource input rate per fish was kept constant. This suggests that interference is due to some other factor or combination of factors. Likely contenders are fish getting in each other's way, obstructing vision and access to food or a requirement for faster lunges at food items which are more likely to be unsuccessful.

This study lends empirical support to Lessells' (1995) challenge to the long-standing assumption that continuous input models require that resource items are consumed immediately upon arrival at a patch. We have shown that it is possible to measure standing crops of resources and that using this method, both interference and exploitation competition can be detected in continuous input situations.

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