

Evolutionarily stable foraging speeds in feeding scrambles: a model and an experimental test

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SUMMARY

An evolutionarily stable strategy (ESS) model of scramble effort (for example, foraging speed) in competition for food or mates, where payoff may depend on competitor density, is described. An individual can increase speed (at some energetic cost) to gain a greater share of resources. The predictions are that if food input per competitor is constant (density independence), the ESS foraging speed should increase with density, but if food input per patch is constant (density dependence), then the ESS foraging speed should decrease with density. The predictions of this model are tested in an experiment using different densities of cichlid fish, *Aequidens portalegrensis*, scrambling for food at a discrete resource patch. The results provide support for the model in a situation where payoffs are density dependent, but fit less well where they are density independent.

1. INTRODUCTION

Competition for a limited resource has important consequences at both an individual and population level. Few evolutionarily stable strategy (ESS) models (Maynard Smith 1982) of competition consider, explicitly, the effects of population density on individual behaviour (Knowlton & Parker 1979; Parker & Knowlton 1980; Parker 1982). Classical game theory models have tended to focus on how the fitness of individuals is affected by the strategy they play, for example, in the 'hawk-dove' and 'war of attrition' models of animal conflict (Maynard Smith 1974). Such models often assume that the value of winning (for example, gaining a food item) is constant, and do not consider the effects of competitor number. Changes in population density can alter the value of winning, with consequences for both individual behaviour and population dynamics (Parker 1985).

Here we present a new scramble competition model which predicts how population density will affect individual strategy, and specifically how it will affect the speed of movement of animals involved in scramble competition. The model is tested experimentally using cichlid fish, *Aequidens portalegrensis* (Hensel), in conditions of varying densities and food input regimes.

2. THE MODEL

The following scramble competition model is essentially a modification of the model of Parker (1985) (see also Godfray & Parker 1992), but with additive costs

and benefits. It is based on a competitive scramble between equal competitors. Competition is solely by exploitation of the resource, which occurs in patches. Without competition, greatest efficiency, in terms of net payoffs, is achieved by expending minimal energy. In the scramble it can pay an individual to sacrifice efficiency to gain a greater share of the resources in a patch.

In the model, individuals occupy a patch into which resource items arrive, and compete in a scramble by increasing their speed of foraging (the model is, however, generally applicable to any form of scramble). Let

n = the number of competitors (or competitor density)

S = the individual's strategy for speed (or other scramble strategy)

R = the (fixed) rate at which resource items are input into the system

$E(S)$ = the energetic cost (per unit time) of searching for food at speed S

$G(S)$ = the net energetic gain (per unit time) of searching for food at speed S .

We assume that an individual can increase its relative share of resource items by increasing its speed, S , if movement is uniform. Explicitly, an individual playing S when its $(n-1)$ competitors play S^* gains food at a rate

$$R [S / (S + (n-1)S^*)].$$

For example, if n is large an individual which doubles its speed virtually doubles its share of the incoming

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resources relative to other competitors. This relation would apply under the assumption of random collision between predators and immobile prey: it is unlikely to apply exactly, but should serve as a fair approximation for many foraging situations. The energetic costs of movement increase with speed, so that E is an increasing function of S . Hence,

$$G(S) = c_1 R [S / (S + (n-1)S^*)] - E(S), \quad (1)$$

where c_1 is the average calorific value of each food item.

To find the ESS speed of foraging S^* (Maynard Smith 1982) let the fitness of a mutant playing $S \neq S^*$ in a population at the ESS be $W(S, S^*_{n-1})$: this is the fitness gained when the mutant plays S against the $(n-1)$ S^* players occupying the same patch. As calorific gains are unlikely to convert linearly into fitness, we allow that

$$W(S, S^*_{n-1}) = V[G(S)], \quad (2)$$

where V is the fitness gain due to a net energy uptake rate of $G(S)$. At the ESS,

$$\begin{aligned} [dW(S, S^*_{n-1})/dS] &= 0; \text{ at } S = S^* \\ [d^2W(S, S^*_{n-1})/dS^2] &< 0; \text{ at } S = S^* \end{aligned} \quad (3)$$

(see Maynard Smith 1982). Substituting (1) into (2) and differentiating as in (3), we obtain

$$dV/dG \{c_1(R/n) \cdot [(n-1)/(nS^*)] - [dE(S^*)/dS]\} = 0,$$

and hence the precise way in which energy converts into fitness (dV/dG) is unimportant, provided that dV/dG is positive (fitness increases with energy intake). Thus

$$S^* = c_1 (R/N) [(n-1)/n] \{[dE(S^*)/dS]^{-1}\}. \quad (4)$$

Note that R/n is the average rate of uptake of food items per competitor, and $dE(S^*)/dS$ is the rate of energy expenditure at the ESS scramble speed.

To analyse (4) more fully we assume that the energy required for movement increases with speed according to the relation $E(S) = 0.5 \rho A S^3 \times 1.2 C_f$ (Wardle & Videler 1980). Where

E = energy

ρ = the density of water

A = the surface area of the fish

S = speed of movement

C_f = the coefficient of friction between the fish and the water.

If we consider all the terms in the equation to remain constant except S then from (4)

$$S^* = \{(c_1 / 3c_2) (R/n) [(n-1)/n]\}^{1/3}, \quad (5)$$

where c_2 is a positive constant = $0.6 \rho A C_f$.

We can use this model to make predictions about the speed of fish movement at different densities for scrambles in which the number of food items available is either proportional to, or independent of, the number of competitors.

The ESS foraging speed, as defined by (5), has the following properties, depending on the nature of input rate of resource items (R):

- (i) R/n constant, if the input rate per competitor is constant, then as competitor density (n) increases, the ESS speed, S^* , increases, as $(n-1)/n$ increases with n ;
- (ii) R constant, if the input rate to the patch is constant, then as competitor density (n) increases, the ESS speed, S^* , decreases, since $[(n-1)/n^2]$ decreases with n .

First consider prediction (i). If input rate per competitor is constant, then at all competitor densities the potential gains are equal. A unilateral increase in speed by one competitor has a greater effect on relative gains at low competitor densities (see equation 1). Hence the ESS speed rises steeply initially, but asymptotes at high competitor density because high unilateral increases yield trivial benefits. This has been termed the 'dilution effect' (Godfray & Parker 1992). Prediction (ii) arises because, if input rate per patch is constant, potential gains decline in inverse proportion to competitor density. Thus, although the dilution effect still applies, the decrease in potential gains overrides it, so that foraging speed declines with competitor density.

These two conditions have some biological plausibility. We can regard R as a fixed property of a given patch. When a group of individuals is constrained to stay together, the R constant condition will apply. When there is no such constraint, however, and individuals are free to move to any part of the habitat at trivial cost, an ideal free distribution (Fretwell & Lucas 1970) is expected, which tends towards constancy of *per capita* gains (R/n constant). Note that an ideal free distribution would actually yield constancy of G rather than R/n : it would act to equalize net payoffs after accounting for scramble expenditure.

Finally, we consider the effect that scramble competition has on 'efficiency', measured as net energy uptake in a given condition. The theoretical expectation is that in both the above treatments, movement per food item gained per competitor should increase with competitor density. Thus 'efficiency' decreases because of competition due to the scramble.

To test these predictions, two experimental treatments simulating (i) and (ii) above were conducted using fish competing for food. In both, the number of fish used was varied from one to ten. In the first treatment the food input remained constant throughout the changes in number of fish. In the second treatment, food input *per capita* remained constant, whatever the number of fish.

3. MATERIALS AND METHODS

A group of the cichlid fish, *Aequidens portalegreensis* were housed in a glass aquarium ($60 \times 30 \times 45$ cm). The water was maintained at a depth of 40 ± 0.5 cm and at a constant temperature of 25 ± 0.5 °C by an internal heater-thermostat. An internal power filter was used to pump water out of the tank. This was returned through a funnel, providing a means by which food items could

be introduced into the tank at a constant rate in a discrete patch. The food items used were flakes of a single type of 'Aquarian' food (P.O. Box 67, Elland, W. Yorkshire). These were standardized for size by sieving, so that all the flakes used were between 5–7 mm diameter. Flake food was used because its slight negative buoyancy meant that it dropped through the water column at the same constant rate as the water flow and also, because the handling time required for each flake was small enough to be considered negligible. That is the fish could easily consume one item and still be able to participate in competition for the following food item.

The fish were fed 10–15 min before each experimental run to reduce inequalities in the relative value of a food item due to satiation state, although this did not appear to affect their readiness to feed during the experiment. Fish were otherwise deprived of food between runs. All the fish used in the experiment were approximately the same size (5 ± 1 cm) and age (16 months).

Seven trials were run with one, two, three, four, six, eight and ten fish. For each replicate, the fish were selected randomly from a group of 20. They were fed for 2 min by dropping single items of food into the funnel at predetermined intervals. Two input rates were used, one representing a situation where input rate, R , was held constant (one item every 5 s), whatever the number of fish and one where input rate per fish (R/n) was held constant at one item / 50 s per fish (i.e. one item / 5 s for ten etc.). Fish behaviour under both regimes was compared. At every input rate all of the fish competed strongly for food. There was no observable difference in the behaviour of any individual, with all fish generally participating in the scramble for each food item. This suggests similar motivation to obtain each food item in all fish. However, the nature of the competition prevented any data from being collected on snaps at food and food items taken, as all fish tended to move around each item obscuring it from view.

A 5 cm-square grid was drawn on the front of the tank, which was illuminated from above. Feeding runs were recorded using a Sony Hi8 video camera mounted in front of the tank. The results were analysed using slow motion and multiple playback of the video recording. Movement was measured, for each individual, by counting the number of squares a focal point of the fish's eye moved into over the 2 min feeding run. There is no reason to believe that there is any directional bias in the fishes' movement. Therefore, this two-dimensional measure (expressed in arbitrary units) was considered to be an acceptable representation of three-dimensional movement.

Overall movement was assumed to consist of two components. First, background movement which would occur regardless of the presence of food. This should be the same for both food input regimes at each density and is, therefore, negligible. Second, there is a component associated with an attempt to gain a food item. If the fish are of equal competitive ability, then each can be assumed to gain the same number of food items. This assumption is supported by actual obser-

vations of the fish. This allowed the movement made per food item gained to be calculated.

4. RESULTS

Mean speed of movement (i.e. squares moved through / 120 s) in each experiment is compared with the model's predictions, determined using equation (5), in figure 1. The experimental results correspond qualitatively with the predictions of the model when R is constant, although the experimental results fit less well when R/n is constant. In the experiments R and n are fixed and S^* is measured, at each density. Therefore we can calculate the mean value of $c_1/3c_2$, from which predicted values of S^* can be calculated. The range of speeds is the S^* predicted from the mean value for $c_1/3c_2 \pm$ the increase or decrease in this value when the constant $c_1/3c_2 \pm$ its standard error was used in the calculation.

To avoid error through pseudoreplication all analyses were performed on data, randomly selected, for one fish per experimental run giving ten replicates for each density. Each replicate being from a different experimental run. The mean movement per item of food obtained per fish at each competitor number for R constant and R/n constant are plotted in figure 2. This shows that as competition increases for each food item, there is a corresponding increase in effort, in terms of level of movement, put into obtaining that item (R constant), whereas when gains remain constant with change in competitor number, movement also remains constant (R/n).

A two-way analysis of variance revealed a significant interaction between fish density and treatment ($F_{1,117} = 193.3$, $p < 0.001$), indicating that the effect of density on movement differed between the two treatments, as follows.

Two subsequent analyses of variance showed that when the gain per food item was density dependent, there was a significant effect of fish number $F_{6,54} =$

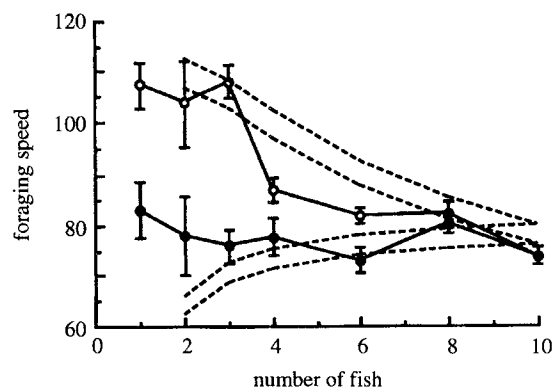


Figure 1. Foraging speed of fish with different food input regimes: Food added in proportion to number of fishes, R/n constant (filled circles) and food of a fixed amount added, R constant (open circles). Values are means \pm standard error for up to five individuals from each experimental run with ten runs for each number of fish. Speed is expressed in terms of the number of squares passed through per two minute trial. Dashed lines represent upper and lower limits for movement rate (mean \pm s.e.), predicted from the model.

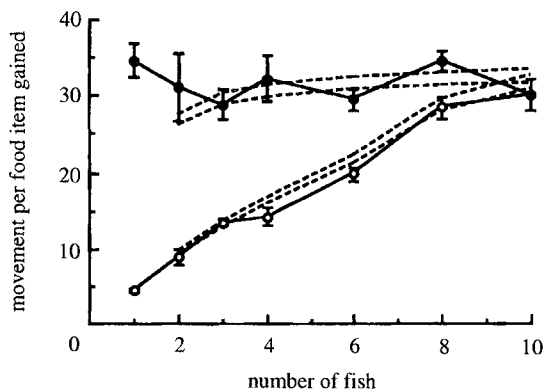


Figure 2. Movement rates of individual fish per item of food gained (S/R) with different food input regimes: food added in proportion to number of fishes, R/n constant (filled circles) and food of a fixed amount added, R constant (open circles). Values are means \pm standard error for up to five individuals from each experimental run with ten runs for each number of fish. Dashed lines represent upper and lower limits for movement rate (mean \pm s.e.), predicted from the model.

70.0, $p < 0.001$, but there was no significant effect when R/n was constant $F_{6,54} = 0.79$, $p = 0.58$. The y -intercept of the R/n constant line is governed by the initial food input regime chosen. In this treatment, food items equivalent to one item / 50 s for one fish were added, so the R/n constant line intercepts with the R constant line where this is at a similar input level, i.e. at one item / 5 s for ten fishes (see figure 2).

5. DISCUSSION

These results provide important empirical support for the scramble model.

1. Foraging speed was highest when potential gains were highest (low densities in R constant condition).
 2. Foraging speed declined with density when R was held constant.
 3. Foraging speed was always lower and less sensitive to competitor density in the R/n constant condition.
- However, we failed to observe the expected increase in foraging speed over low competitor densities in the R/n constant condition.

The experimental system closely supports the main assumptions of the model. Competition, in this system, is via scramble competition, solely through exploitation of the resource. Very little aggression was exhibited between individuals during experimental runs. Although more mature fish do become territorial and exhibit a high degree of aggression towards conspecifics, the fish used in this study were young enough to coexist peacefully. As the number of competitors increases, interference and aggressive displacement may play a more important role, although this did not seem to be the case in this experiment.

Food is added to the tank at a point source, thus aggregating the resource. *Aequidens portalegreensis* was chosen for this study, as young fish are non-territorial and compete strongly for food. Both sexes provide a high degree of parental care, which leads to near equality between the sexes in terms of the payoff

associated with each food item. Throughout the experiment, it was assumed that fish were similar in their motivation to feed and also in their satiation state. The nature of the competition prevented data being collected on the number of food items consumed and snaps at food – because all fish gathered round each food item – lunging and snapping simultaneously. Some qualitative support can be gained for the assumption of equality between fish from this observed similarity in behaviour.

The metabolic cost of increasing swimming speeds follows a J-shaped curve (Wardle & Videler 1980; Videler 1993). Thus any increase in speed is associated with a corresponding increase in cost. In short swimming bouts, such as those employed in the scramble for food in this experiment, fish rarely move with a constant velocity. Mean movement rate is used to represent fish swimming speed, although this is obviously an approximation because none of the fish maintained a constant swimming speed throughout the feeding run. There is evidence to suggest that fish actually search and feed in a saltatory search pattern (O'Brien *et al.* 1990). Here, mean movement rate could be increased by reducing the time spent stationary.

This study complements previous models of fish swimming speeds, such as Ware's model (1978) which considered solitary fish and the speed at which they should swim to maximize growth rate. Our study incorporates density-dependence, which has implications for many social species.

Long term studies on roach (*Rutilus rutilus* L.) (Koch & Wieser 1983) have shown that there is a trade-off in energy partitioning between the development of gonads and the level of movement: this further supports the assumption that the energetic budget of the fish is balanced between feeding effort and parental investment.

At high population densities there is, therefore, a decrease in overall efficiency in the R constant condition, as more movement is required to obtain each food item. This contrasts with the situation where R/n remains constant. In this case, the number of competitors can increase indefinitely without a significant effect on the effort required to gain each food item by any individual. However, at higher competitor numbers constraints such as space available and aggression between individuals will operate to limit the number of competitors able to exploit that patch, as new competitive mechanisms such as interference come into play.

The model predicts a lower rate of movement at low competitor numbers, when R/n is constant, than was observed in the experiment. This could be a result of the model's assumption that fish only move to obtain food items. In reality, however, it is likely that the fish have a baseline level of movement onto which increases due to foraging are superimposed. If this baseline were higher than the model's predicted speed of movement, then it could account for the difference in observed and predicted movement speeds. Experiments examining the competitive abilities of fish and also measuring the baseline level of movement would be valuable in further interpretation of the experimental results.

These results lend support to the main predictions of the model, confirming that individual efficiency can be density dependent and that the competitive strategy employed by individuals may therefore have consequences at the population level.

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