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COMPETITIVE INTERACTIONS IN SOCIAL FORAGERS

Stuart Humphries



UNIVERSITY
of
GLASGOW

This thesis is submitted for the degree of Doctor of Philosophy,

Division of Environmental and Evolutionary Biology,

Institute of Biomedical and Life Sciences,

Faculty of Science,

University of Glasgow

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CANDIDATES DECLARATION

I declare that the work recorded in this thesis is entirely my own, except where otherwise stated, and that it is of my own composition. Most of the material included in this thesis has been produced in co-authorship with others and has been presented for publication. My personal contribution to each results chapter is as follows.

2. *Published as:* Humphries S., Metcalfe N.B. & Ruxton G.D. 1999. The effect of group size on relative competitive ability. *Oikos* 85: 481-486. The idea was jointly developed by all three authors. SH performed all experimental work and analysis, and was senior author of the manuscript.
3. *In press as:* Humphries S., Ruxton G.D. & Metcalfe N.B. Group size and relative competitive ability: geometric progressions as a conceptual tool. *Behavioral Ecology and Sociobiology*. The idea was jointly developed by all three authors. SH performed all experimental work and analysis, developed the model and was senior author of the manuscript.
4. *Published as:* Humphries S., Ruxton G.D. & Metcalfe N.B. 1999. Patch choice and risk: relative competitive ability is context dependent. *Animal Behaviour* 58: 1131-1138. The idea was jointly developed by all three authors. SH performed all experimental work and analysis and was senior author of the manuscript.
5. *Submitted to the American Naturalist as:* Humphries S. & Ruxton G.D. Unequal competitor ideal free distributions: predictions for differential effects of interference between patches. The idea was developed jointly by SH and GDR. The model was developed by SH who performed all the analysis and was senior author of the manuscript.
6. *Submitted to the Journal of Animal Ecology as:* Ruxton G.D., Humphries S & Farnsworth K.D. The IFD with non-competitive between-individual differences. The paper was developed jointly all three authors. The analysis and manuscript preparation were performed jointly by GDR and SH.
7. *Published as:* Ruxton G.D. & Humphries S. 1999. Multiple ideal free distributions of unequal competitors. *Evolutionary Ecology Research* 1: 635-640. The idea was developed jointly by SH and GDR. GDR carried out the analysis, and the manuscript was written jointly by SH and GDR.

8. *Published as:* Ruxton G.D., Armstrong J.D. & Humphries S. 1999. Modelling territorial behaviour of animals in variable environments. *Animal Behaviour* 58: 113-120. The ideas behind the manuscript were developed by GDR and JDA, who jointly developed a model and wrote a manuscript. After an earlier GDR and JDA manuscript was rejected, SH was invited to carry out more simulations. However, following this analysis, it became apparent that it was necessary to completely rewrite the model and the manuscript. The new model was developed by SH who also carried out the analysis and wrote the central section of the manuscript. The Introduction and Discussion were written jointly by all three authors.

9. Assessing the oddity effect: the role of body size and competition. The original idea regarding competitive differences in relation to Peuhkuri's work was SH's and a manuscript was developed on this theme with GDR. Concurrently, Daniel Hoare and Jens Krause were working on a manuscript discussing the same problems from the perspective of differential weight loss. After contact with DH and JK it was decided that the two manuscripts should be combined onto one. The ideas for elaboration of the work were developed jointly by SH and GDR.

I further declare that no part of this work has been submitted as part of any other degree.



Stuart Humphries
September 1999

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ABSTRACT

Empirical and theoretical investigations of aspects of the ideal free distribution (IFD) are presented, with particular emphasis on interactions between individuals within foraging groups. An overview of the theory is presented, and the implications of the work included in this thesis to ideal free distribution theory are discussed.

The effect of group size on the relative competitive ability of individual fish within a foraging group is shown to be dependent upon the difference in body size between two focus individuals in a group, but this difference itself has no direct effect on relative competitive ability. A subsequent empirical test of a novel mathematical tool reveals that there is no simple general rule for describing how relative competitive ability will change with group size, and that very specific knowledge of the system under study is needed in order to produce robust predictions.

The relative abilities of individual cichlids to obtain food under scramble competition are shown to be highly repeatable between trials. However, when given a choice between two patches differing only in their temporal variability in input about an identical mean, an individual's rank based on intake in one patch was uncorrelated with either its intake in the other patch or its intake in either of two different trial types. The basis for, and consequences of, this dependence of relative competitive ability on the context of the foraging situation are discussed.

The general case (previously unexplored in the literature) where the effect of interference can vary between patches is examined. Simulations from an individual-based model reveal a decrease in the number of stable equilibrium distributions as the competitive advantage of the dominant phenotype declines in one patch, leading eventually to a single stable equilibrium, in which both phenotypes are found on both patches. Such a dynamic pattern of distributions is not predicted by classical interference IFD theory and its relevance to a lack of predicted distributions in certain empirical tests of the theory is discussed.

A model of the IFD is presented where differences between phenotypes other than those involved in direct competition for resources are considered. It is shown that these post-acquisitional differences can have a dramatic impact on the predicted distributions of individuals. The distributions produced when these post-acquisitional traits are considered mirror those that examine direct competitive traits. This comparison illustrates that individual differences still exert considerable influence on the distribution of the individuals concerned, irrespective of whether they are expressed before or after competition for resources.

An individual-based model of the IFD is presented. If individuals move only so as to improve their resource gathering rate, then the system settles to one of a finite number of equilibria. Contrary to the predictions of a previous study in the literature (Hugie & Grand 1998), occasional switching of a randomly-selected individual between resources does not lead to this distribution of equilibria collapsing to a single point. In fact, the introduction of random switching can induce the population to periodically shift between equilibria, thereby increasing spatio-temporal variation in competitor numbers.

An individual-based model describing the distribution and resource gain of territorial individuals in situations where the rank order of territory quality changes over time is presented. The model integrates both competitive (territory holding ability) asymmetries and a memory function. Results indicate that there is a balance of effects resulting in a peak in movement rates, but not resource gain, for individuals of intermediate ability. Furthermore, when the system is reduced to a linear array of territories (as commonly used in empirical studies) the model generates quite different predictions because of the severe limitation in movement that the linear array imposes.

Results from an experimental test of the oddity effect (Peuhkuri 1998), which evaluates whether individual fish adjust their perceived predation risk in relation to their relative 'oddity' within a foraging group, are discussed. Alternative explanations to some of the results given are suggested, in an attempt to illustrate the complexity of the situation and to provide a framework on which future investigation of this subject can be based.

GENERAL INTRODUCTION

Knowing where animals are likely to be at any particular time is of considerable importance to ecology. On its simplest level, predicting the distribution of animals has uses in conservation, feeding and reproductive biology, as well as community and population ecology. However, it is in the field of behavioural ecology that one particularly useful method has flourished. The idea that animal distributions can be explained by consideration of the individuals involved (a 'bottom-up' approach) has, in the last three decades, been borne out as one of the cornerstones of the field (Milinski & Parker 1991, Tregenza 1995).

Despite often extensive violation of its key assumptions in the systems it describes, and the proposal of a number of alternatives, one method of prediction has proved particularly successful. As a result, the study of animal distributions has been dominated by ideal free distribution theory (Fretwell & Lucas 1970, Fretwell 1972, see also Brown 1969, Orians 1969, Parker 1970, Parker 1974). It has been the basis for hundreds of papers covering a broad range of areas and organisms since it was first introduced, and has often been the focus of intense discussion and debate (e.g. Kennedy & Gray 1993, Gray & Kennedy 1994, Milinski 1994, Rita & Ranta 1999, Sutherland & Parker 1999). The ideal free distribution (IFD) provides us with a conceptually simple, but remarkably accurate, way of describing the distributions of animals in time and space on the basis of individual decisions and behaviours.

In its simplest form, the IFD describes the distribution of a number of identical individuals that are 'ideal' (they are omniscient and so know everything about their environment), and 'free' (to travel anywhere within that environment without cost or restriction). These 'ideal free' animals decide where to go within their environment based on a simple rule of maximising their resource acquisition (gain) rate. The principal process of Fretwell and Lucas' IFD is that the 'suitability' of a patch decreases as the density of searching animals on that patch increases. Consequently, in an environment containing several patches differing in suitability, the first competitors to arrive will choose to occupy the best patch. As more individuals arrive, density dependent effects on the better patch will lead to previously poorer patches becoming equally suitable and thus leading to an equilibrium at which all

patches give the same resource acquisition rate and no individual can gain by moving to a different patch. IFD theory usually considers a surrogate for the suitability of a patch, and fitness correlates commonly used in this capacity include parameters such as food intake rate or mating success.

Continuous input models

Simply sharing resource items between individuals on a patch can produce the requisite density dependent effects on individuals' resource acquisition rates. This situation occurs if resources are introduced continuously to a patch and are utilised as soon as they arrive, the 'continuous input' case (Sutherland & Parker 1985, Parker & Sutherland 1986). Examples of this kind of situation include fish foraging for drifting prey in a stream (Milinski 1988), male dungflies (*Scatophaga stercoraria*) competing for arriving females (Parker 1970, Parker 1978), or lekking birds (Alatalo *et al.* 1992). In the continuous input case an individual's gain rate will depend on both the input of resources into the patch and the number of other individuals competing for those same items. Considering these simple rules, the assumptions of the basic IFD model can be reiterated as follows:

- i) all the individuals in the habitat are identical,
- ii) the habitat contains a number of resource patches that vary in fitness value (suitability) to the competitors,
- iii) the competitors can move freely between patches within the habitat without cost or restraint, and each individual moves to the patch where its expected gain is highest,
- iv) as the number of competitors exploiting a patch increases, the fitness value of that patch declines in inverse proportion to the number of competitors present on it.

In most ideal free models, it is assumed that this density dependence is manifested as a continuous, monotonic decline in fitness with increasing numbers in the patch, an assumption made mainly for mathematical tractability (Milinski & Parker 1991). It is from the assumptions that the two basic predictions of the model arise:

- i) all competitors experience equal gains, independent of the patch that they are in, and
- ii) average gain rates are equal in all occupied patches.

Using the ideas of fitness correlates and linear density dependence, the general verbal theory of Fretwell and Lucas (1970) can be described in more rigorous terms. If we consider n individuals in a habitat consisting of several patches, each with a different resource input rate Q , then an individual's rate of gain W in patch i is

$$W_i = Q_i / n_i \quad (1)$$

Where n_i represents the number of individuals on patch i . As the ideal free distribution is an equilibrium where fitness is equal, irrespective of patch, the gain of individuals in each patch must satisfy

$$W_1 = W_2 = W_3 \dots W_i = C \text{ (constant) for all patches} \quad (2)$$

which allows us to determine that the number of individuals in a given patch will be

$$n_i = Q_i / C \quad (3)$$

Thus, the number of competing individuals in each patch will be directly proportional to the rate of input of resources to that patch. This known as the 'input matching rule' (Parker 1978) or 'habitat matching rule' (Pulliam & Caraco 1984) and is the third prediction of the IFD for continuous input situations.

Interference models

A second situation where the number of individuals on a patch can affect an individual's rate of gain is that of 'interference'. Interference is generally defined as a short term, reversible, decline in an individual's gain rate due to the presence of others (Goss-Custard 1980). Interference usually arises through competition, but in a slightly different way to that seen in the continuous input case. In this case, individuals are limited in their search time as well as by the abundance of resources (Tregenza 1995). Thus, the mere presence of another individual on a patch may cause a reduction in the focus individual's gain rate if it causes that individual to spend less time searching for resource items (e.g. Cresswell 1997). Examples of such

interference competition commonly cited include disturbance of prey by conspecifics (e.g. redshanks, *Tringa totanus*, feeding on the amphipod *Corophium volutator*, Goss-Custard 1970), kleptoparasitism where individuals steal resource items from others (e.g. oystercatchers, *Haematopus ostralegus*, feeding on mussels *Mytilus edulis*, Goss-Custard *et al.* 1984), and fighting between individuals (e.g. fights between knots, *Calidris canutus* become more frequent when the birds are close together, Goss-Custard 1977). Integrating the concept of interference into simple IFD models has historically been most commonly achieved using Hassell and Varley's (1969) 'interference constant' m as proposed by Sutherland (1983). Sutherland suggested that this interference constant be incorporated into the IFD model (equation 1) thus:

$$W_i = Q_i / n_i^m \quad (3)$$

where $0 \leq m \leq \infty$, such that when m is zero there is no interference. In this case Q_i is equal to the maximum gain that an individual would gain in the absence of competitors. Again, in order to fulfil the ideal free equilibrium, the gain for all individuals must be constant for all patches, thus

$$W_i = Q_i / n_i^m = C \text{ (constant) for all patches} \quad (4)$$

such that the numbers of competitors in a given patch i will be

$$n_i = (Q_i / C)^{1/m} \quad (5)$$

The predictions arising from this interference based ideal free model differ from those for the continuous input model. The scaling of gain using this method of density dependence means that when there is little or no interference (i.e. m tends to zero) all competitors will be found in the best patch, as their gain rate is unaffected by the presence of others (but see Doncaster 1999 for a reinterpretation of this particular situation). However, when interference is present, the number of individuals on a patch will tend to increase until the effect of interference reduces

their average gain to a point where it will pay some individuals to move to the next best patch. Thus, as in the continuous input case, the equilibrium distribution is reached when the gain of all individuals is the same, independent of patch. In the case of very strong interference (i.e. $m = 1$) competitors should be distributed in the ratio of patch profitabilities as seen in the continuous input model.

Unequal competitor models

Empirical tests of IFD theory have covered a broad range of species and resources. For example, continuous input IFDs have been examined in dungflies, *Scatophaga stercoraria*, (Parker 1978), sticklebacks, *Gasterosteus aculeatus* (Milinski 1979, 1984a), Loricariid catfish (Power 1984), cichlids, *Aequidens curviceps* (Godin & Keenleyside 1984), and mallard ducks, *Anas platyrhynchos* (Harper 1982). Interference IFDs have been looked for in oystercatchers, *Haematopus ostralegus* (Sutherland 1982, Goss-Custard *et al.* 1984), herring gulls, *Larus argentatus* (Monaghan 1980, Sibly & McCleery 1983), and white-footed mice, *Peromyscus leucopus* (Morris 1989). In general, tests of the continuous input and interference IFD models have been largely successful (see Parker & Sutherland 1986, Milinski & Parker 1991 and Tregenza 1995 for reviews). However, as Parker and Sutherland (1986) realised, many of these first studies violated the basic IFD assumption of equal competitive abilities and, in the case of interference, that of equal average gain on each patch. Thus, the prediction of equal gains for all individuals was not upheld. An individual's competitive ability is generally considered to be a measure of its ability to obtain resources. This ability is likely to vary between individuals and even within an individual over time (Tregenza 1995). Competitive ability has been shown to vary with a number of factors, the most common being size, age and/or experience, and aggressiveness, across a wide range of taxa, (e.g. fish Milinski 1982). The influence of parasitic infection on competitive ability is another issue currently generating a great deal of interest (Crowden & Broom 1980, Milinski 1984b, Cunningham *et al.* 1994, Barber & Ruxton 1998).

To allow for such individuality, Parker (1982) introduced a simple modification of IFD theory that considers differences in relative competitive ability between two different phenotypes. In his model, each phenotype is assigned a 'competitive

weight' as a measure of its *relative* competitive ability, and receives payoffs in the ratio of these relative competitive abilities. For instance, if phenotype *A* has twice the competitive weight of phenotype *B*, it gains twice the resources of *B* in the same patch. Competitive weights were quickly incorporated into models dealing with unequal competitors of multiple phenotypes (Sutherland & Parker 1985, Parker & Sutherland 1986, Sutherland & Parker 1992) where the resources acquired by an individual are dependent upon its competitive weight relative to the mean or total competitive weight within the patch.

The concept of competitive weights has been applied widely in IFD theory and is now an integral part of the majority of new IFD models and tests. It has been used in both continuous input and interference models of the IFD to produce predictions that comprise the basis of most empirical tests of the theory (see Tregenza 1995 for a comprehensive review). Sutherland and Parker (1985, Parker & Sutherland 1986, 1992) have provided the basic theoretical framework using two models: the unequal competitor continuous input model, and the unequal competitor interference model. These two models provide clear predictions for the distribution of unequal competitors between multiple resource patches. For the continuous input case the unequal competitor model predicts a range of possible equilibria, the number of which are as numerous as the number of competitors involved. These stable equilibria all feature one common rule: that the ratio of resource input to total competitive weight on the patch is equalised for all patches, i.e.

$$\frac{Q_1}{K_1} = \frac{Q_2}{K_2} = \frac{Q_3}{K_3} \dots \frac{Q_i}{K_i} = C \text{ (constant) for all patches} \quad (6)$$

where K_i is the total competitive weight in patch i . Thus, the gain of a competitor of phenotype A on patch i will be

$$W_{Ai} = ((K_{Ai}/K_i)Q_i)/n_i \quad (7)$$

where W_{Ai} and K_{Ai} represent the gain and competitive weight respectively of phenotype A on patch i . Thus, each individual receives the proportion of resources

equal to its proportion of the total competitive weight in the patch. Importantly, these proportional differences in gain (relating to the concept of *relative* competitive ability) remain constant across patches with different input rates and competitor densities. The fit of empirical data to the basic (equal competitors) IFD (see above) despite violation of the assumption of equal competitive abilities has been most convincingly explained by simple probability: the distribution most frequently seen in experiments is the one most likely if the equilibrium is selected by chance (Sutherland & Parker 1985, Houston & Mcnamara 1988, Milinski & Parker 1991). However, several other possibilities may also add to the occurrence of this particular distribution, and these are discussed in detail by Tregenza (1995).

For interference situations, the unequal competitor model of Parker and Sutherland (1986) again scales the effect of competitor density by using m , the interference constant. Because the relative competitive ability of an individual affects the relationship between competitor density and gain, it is now m that is scaled by the ratio of competitive weights:

$$W_{Ai} = Q_i n_i^{-m(K_i/K_{Ai})} \quad (8)$$

In this model the gain of individuals of low competitive ability is reduced more by increased density on a patch than that of individuals of higher competitive ability. Consequently, poorer competitors will tend to do better in patches containing fewer competitors and the relative gains of different phenotypes will vary between patches of different quality and therefore different competitor density. Patches with higher resource densities will thus have more competitors on them, leading to higher interference in these patches. Subsequently, the prediction for the unequal competitor interference model is that better competitors will have their highest gain rate in these high resource, high interference patches. Conversely, poor competitors will do best in low interference patches, leading to a situation where there is an absolute correlation between competitive ability and patch quality. This is the 'truncated phenotype distribution' (Sutherland & Parker 1985, Parker & Sutherland 1986, Sutherland & Parker 1992), in which no more than one phenotype can mix across two patches (i.e. individuals of this phenotype do equally well on both patches). A

perfect truncated phenotype distribution has been difficult to find in reality (e.g. Bautista *et al.* 1995, Milinski *et al.* 1995), and is considered unlikely to occur due to a number of different reasons (see Parker & Sutherland 1986, Milinski & Parker 1991, Milinski *et al.* 1995). It should be noted that the predictions presented here only stand for situations where relative gain is constant across different patches. Relaxation of this ‘assumption of constancy’ has only been considered for continuous input cases (Parker & Sutherland 1986, Sutherland & Parker 1992) and is discussed further in **chapter five** where I examine predictions from a model that relaxes the assumption for interference situations. Alternatives to Sutherland and Parker’s unequal competitor models have been put forward, two of which (Korona’s (1989) approach based on pairwise interactions, and Holmgren’s (1995) separation of competitive ability into distinct components), provide different predictions from those outlined above, and are described in more detail by Tregenza (1995). A third alternative, van der Meer’s (1997) interaction-matrix method is discussed in more detail in **chapter five**.

Aims and objectives of the current study

A common feature of many modifications of IFD theory is that they tend to replace some of the assumptions that have been shown to be inappropriate with other potentially contentious ones. The assumptions of these new models can be additional to those already in place, or may simply put more emphasis on those that already exist. The problem with this approach is that many of the assumptions made by modified IFD models are unjustified, and at best simply untested. Such detachment of theory from empirical work is a growing problem for IFD theory and the aim of this thesis has been to address some of the current assumptions made by the theory using both empirical tests and theoretical investigation.

The first part of this thesis presents work which challenges the idea that relative competitive ability is not influenced by group size (**chapters two and three**) or context (**chapters four to six**), both of which have been ignored in most examinations of the IFD (Tregenza 1995, Tregenza *et al.* 1996, Tregenza & Thompson 1998). Recently, work has shown that there are also important situations that cannot be covered by IFD theory, such as movements made between patches

that are not related to resource gain, territoriality, and the concept that some animals tend to form assorted social groups whilst searching for resources. These ideas are examined in the second part of the thesis (**chapters seven to nine**).

The effects of increases in competitor density have sometimes been found to differ between good and poor competitors, with better individuals suffering less in terms of gain (Coates 1980, Rubenstein 1981). This violation of the assumption of constant competitive ability was examined by Tregenza (1996, Tregenza & Thompson 1998) who found differences, but no general trends. In **chapter two** I confirm that in shoals of foraging minnows (*Phoxinus phoxinus*), relative competitive ability does vary with group size. More importantly, I show that there are separate trends for these changes, which are dependent upon the size difference within the pair of individuals being examined. **Chapter three** follows on from this work, using a theoretical approach which is tested against empirical data from foraging three-spine sticklebacks. In this chapter I develop a mathematical model which can be used to describe and quantify changes in relative competitive ability between pairs of competitors which occur due to changes in the size of the foraging group.

Chapter four again deals with the assumption of constant relative competitive ability, but this time I examine competitive differences between individuals in contrasting foraging situations. This chapter is based on experimental trials involving cichlid fish (*Tilapia zillii*) foraging on two types of patch. The fish were observed foraging on each patch singly, as well as being given the choice between both types of patch present in the same tank simultaneously. It appears from this work that an individual's relative competitive ability is also dependent upon the foraging situation it finds itself in, and that some individuals may be more suited to a particular situation than others.

Chapter five is a theoretical examination of an unexplored case of the unequal competitor interference IFD model. Here, an individual-based model is used to explore the predictions for an IFD case where the effects of interference differ between patches. I use a method of describing interference based on van der Meer's (1997) interaction-matrix method and compare it to predictions generated using the

classical Sutherland-Parker model of interference. A mathematical approach is used in **chapter six** to explore how non-competitive differences between individuals, for example in digestion or energy efficiency, can affect the equilibrium distributions produced as a result of 'standard' ideal free theory.

The idea that movements between patches that are unrelated to the resource being considered by an experimenter may affect a distribution's fit to the IFD is well recognised (Tregenza 1995). Indeed, it has been shown to occur in guppies (Abrahams 1989), where males distribute themselves between two food sources based on both the food availability and the presence of another resource (in this case females). Other interactions within groups may cause movements other than those carried out for foraging, especially when predation risk to foraging individuals is considered. A recent challenge has been that previous models of the IFD may not be realistic enough as they do not usually consider such non-IFD movements. In **chapter seven** I use an individual-based model to illustrate the finding that one prediction made for a model incorporating non-IFD movements (that these movements will produce a single, stable distribution, (Hugie & Grand 1998)) is not generally true.

Although the IFD is a useful tool for predicting the distributions of animals feeding in cohesive groups, or when there is little aggression between individuals, it performs poorly when despotic behaviour is present. In **chapter eight** I present an individual-based model for describing animal distributions where antagonistic interactions between individuals result in the formation of territories.

Chapter nine discusses the effects of size differences between individuals in a group on their perception of predation risk. The idea that individuals may prefer to associate with others of a similar size, owing to an increased risk of predation if they 'stand out from the crowd' (Pitcher *et al.* 1986, Ranta & Lindstrom 1990, Ranta *et al.* 1992) is known as the 'oddity effect'. The costs of this oddity may manifest themselves in extra time spent in anti-predator vigilance by the odd individuals and this chapter discusses one such test of this idea (Peuhkuri 1998). The chapter puts forward an alternative reason for observed differences in the foraging rate of

differently sized fish to that proposed by the original paper's author, suggesting that differences in size-related differences in weight loss and competitive ability may be involved.

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THE EFFECT OF GROUP SIZE ON RELATIVE COMPETITIVE ABILITY

Abstract

Recent influential models of the distribution of foraging animals have recognised the importance of individual variation in competitive ability, but have assumed that this property is intrinsic to the individual. However, Tregenza *et al.* (1996) suggested that in continuous input situations (where resources are supplied at a steady rate and utilised immediately) the relative competitive ability of an individual may be affected by competitor density. We therefore examined the effect of group size (which was equivalent to competitor density) on relative competitive abilities within a shoal of European minnows (*Phoxinus phoxinus*, L.) exploiting a single, continuous-input food patch. In partial agreement with Tregenza *et al.* and in contrast to Sutherland and Parker's 'Phenotype scales intercept' model of the ideal free distribution (IFD) with competitive asymmetries, we found two processes that act in opposite directions. These effects can cancel each other out to give the misleading idea that there is no effect of group size upon relative competitive ability. These effects were dependent upon the difference in body size between the two fish in a pair, but this difference itself had no direct effect on relative competitive ability. The reasons for the differences between our results and those of Tregenza *et al.* are discussed.

Introduction

Since its inception in the late 1960's and early 1970's, the concept of the 'ideal free distribution' (IFD) (Fretwell & Lucas 1970) has generated considerable interest from behavioural ecologists trying to predict the distribution of animals in an heterogeneous environment. In its simplest form, the IFD predicts that animals of equal competitive ability which are 'free' to travel anywhere in the environment without time or energy costs and 'ideal' in that they have complete knowledge of their environment, will go to those patches where they are able to maximise their resource gain. In an environment with more than one resource patch, density-dependent effects will lead to an equilibrium at which all patches provide an equal resource acquisition rate and consequently no individual will be able to gain by moving to another patch.

Despite near universal violations of its key assumptions, the IFD has paradoxically been considered to be one of the most successful predictors of animal distributions to date (Talbot & Kramer 1986, Milinski 1988, Krebs & Davies 1991). Various empirical investigations have revealed that one of the major assumptions of the IFD - that competitors are all equal in terms of competitive ability - is rarely met in practice (Sutherland *et al.* 1988). Several IFD models have been put forward that allow for these differences in competitive ability (Sutherland & Parker 1985, 1992, Parker & Sutherland 1986, Korona 1989, and reviewed in Tregenza 1995 and Tregenza *et al.* 1996) but these models, although allowing the relaxation of the assumption of equal competitive abilities, often substitute other potentially contentious assumptions. The most commonly used models that allow for these competitive asymmetries are those developed by Sutherland and Parker (Sutherland & Parker 1985, 1992, Parker & Sutherland 1986) to describe two alternate ways in which the relative resource acquisition rates of phenotypes differing in competitive ability may vary with competitor density: the 'phenotype scales intercept' and 'phenotype scales slope' models. These names relate to the results of the two models plotted as a graph of $\log(\text{intake rate})$ against $\log(\text{competitor density})$: in the former the competitive ability of the phenotype affects the gradient of the line, whilst in the latter it is the intercept of the line which is affected (for a more detailed discussion see Tregenza 1995

pp263-269 and figures therein). Thus, in the 'phenotype scales intercept' model relative competitive ability is predicted to remain constant at all densities, whereas in the 'phenotype scales slope' model good competitors are predicted to do proportionally better than poor ones as density increases. The predictions of the 'phenotype scales intercept' model are thought to best fit the results of previous studies of the IFD where the food supply is continually being replenished ('continuous input' situations; Sutherland and Parker 1992).

Tregenza *et al.* (1996) conducted an empirical test of the assumption that relative competitive ability was unaffected by the density of competitors involved in the interaction. They found a decrease in the difference between individual intakes as density increased, rather than the constant or increasing difference predicted by Sutherland and Parker's two alternatives. Tregenza *et al.* (1996) suggested that in continuous input situations the reduction in differential foraging success between individuals as density increased was due to a transition from contest competition at low densities to scramble competition at higher densities. The effect of competitor density on the relative competitive ability of an individual would therefore be more complicated than had previously been thought.

Here we report on an experiment designed to explore this suggestion in more detail. In order to test if Tregenza *et al.*'s conclusions hold more generally, we used a similar continuous input situation, but utilised only a single patch and looked at the ratios of intake rates of individually identifiable pairs of fish rather than using two patches. Comparisons of relative competitive ability were made over the whole group in order to simplify the analysis and to reduce the risk of memory effects influencing the results. Instead of Tregenza *et al.*'s use of what was effectively a point source for the input patch we utilised a set-up designed to produce a more dispersed patch, and used a constant size of food item in order to standardise the energetic gain per item. Group size was controlled in our experiment, compared to Tregenza *et al.*'s reliance on fish moving at will between patches. We also took the view that treating each item of food as a discrete opportunity for competition risked pseudoreplication and so decided to treat only the overall mean feeding rates of each

member of a pair of fish in a single trial as a discrete datum. To further reduce the risk of pseudoreplication from the use of a limited number of fish we designed the pattern of trials so as to minimise previous knowledge of competitors outside the pairs.

Methods

A group of sixteen European minnows (*Phoxinus phoxinus*) chosen from a batch collected from the River Endrick, Stirlingshire, Scotland, were used in these experiments. All fish had been in captivity for a minimum of six months in glass stock tanks at $8.5 \pm 1^\circ\text{C}$ with a 12L/12D light cycle; these conditions were maintained throughout the experiment. The fish were individually marked under anaesthesia using unique combinations of Alcian blue dye marks on the dorsal and anal fins and on the two lobes of the caudal fin. Marking was accomplished by introducing the dye into the fin rays of the anaesthetised fish via a Repette injector system (Jencons (Scientific) Ltd.). Whilst under anaesthetic, the fish were also weighed and measured (standard length, SL). The fish were then divided into eight pairs, which were kept in separate 3 litre glass tanks with a gravel substrate and an airstone. Screens between the containers maintained visual isolation of the pairs.

The two arena tanks were all-glass aquariums measuring 610×307×295 mm (L×W×D), with a water depth of approximately 200mm. The arena tanks had a white back to increase contrast and opaque sides with the front left clear for viewing. The bottom of the tanks was covered with a translucent plastic covering that allowed easy cleaning of the bottom of the tank whilst still giving the fish a textured substrate that prevented them from becoming overly stressed. In addition, each arena tank contained an air-powered sponge filter and a powerhead to supply water to the feeder (see below). The arena tanks were screened off from the rest of the room using black polythene sheeting to avoid visual disturbance.

Over a six day training period prior to the main experimental trials, each pair of fish was temporarily transferred to one of the arena tanks to be fed once a day. One of these tanks was initially empty whilst the other already contained four extra minnows

of approximately the same size as the experimental fish, to let the pairs get used to feeding in larger groups. Pairs were introduced to the two types of arena tank on alternate days and in a different order each day. After the training period was completed, the pairs were fed to satiation with frozen Chironomid larvae and then fasted for three days before the first experimental trial, in order to standardise their hunger levels. A period of three days was chosen to allow the fish to evacuate their upper gastro-intestinal tracts of food before the first trial (Russell & Wootton 1992), thus standardising hunger and motivation to feed.

Each trial consisted of moving the pairs of fish to the test arena, leaving them for 30 minutes to settle, then feeding the fish 150 pellets (which took approximately 23 minutes). After each trial the fish involved were moved back to their holding containers before being fed to satiation with frozen Chironomid larvae. Trials were carried out every fourth day to allow for evacuation of the foregut as mentioned above. Trials were conducted so as to minimise previous knowledge of the other pairs in the experiment: the first round of trials involved two groups of eight fish (pairs one to four and pairs five to eight); the second, four groups of two fish (pairs three, four, seven and eight) and two groups of four fish (pairs one and six and pairs two and five); the third round was similar to the second with pairs one, two, five and six tested separately and two groups of four fish comprised of pairs three and eight together and pairs four and seven together; the final round was for a group size of 16 fish, where all pairs were used to make up the group. During feeding trials the fish were fed pellets made from trout food (BOCM Pauls Fulmar Feeds). The trout food was ground and mixed with water and the resulting thick paste placed in a computer-driven pellet extruder (Figure 2.1). Every $9.0 (\pm 0.05)$ seconds a stepper motor pushed a threaded rod a fixed distance into the plastic syringe, so extruding a pellet of constant size (1.7×2.1 mm, weighing 5.4 ± 0.6 mg) from the syringe. The pellet was then sliced off with a blade and blown by a jet of compressed air into the funnel containing flowing water. The water then carried the pellet into the tank, first pouring over a shallow plastic dome (65mm diameter) mounted just above the water surface. This dome acted to spread the water flow so that the position at which the pellet

entered the tank was made less predictable, thus hindering one fish from monopolising a point food source.

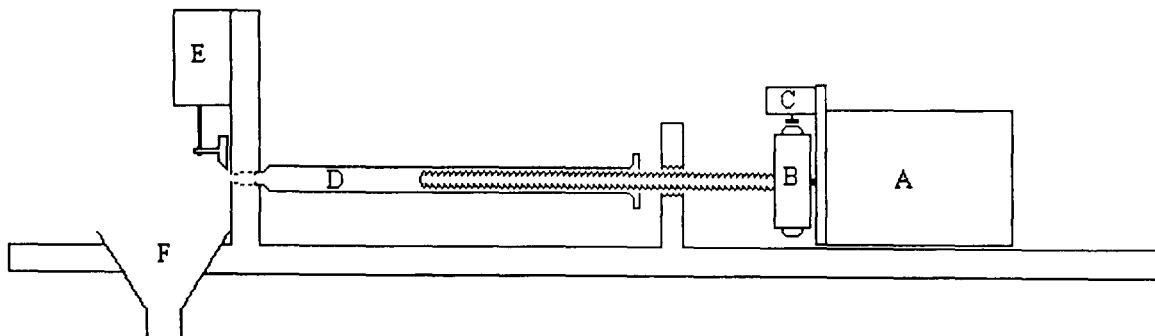


Figure 2.1. Diagram of the extrusion feeder used in the experiments. (A) 12v motor, (B) cam and threaded rod, (C) microswitch (activated by cam) to control number of turns of the rod, (D) 1ml disposable syringe containing food paste, (E) solenoid driving cutting blade, and (F) funnel to catch pellet and direct it down onto the spreader, which is at the water surface of the tank.

Trials were filmed using a Panasonic NVMS95 VHS video camera with wide-angle lens. The resulting video tapes were analysed in slow motion to allow accurate determination of individual intake rates over 70 pellets in each trial starting at, and inclusive of, the first pellet to be consumed; later pellets were excluded as some fish began to reach satiation after this point. Pellets were also excluded from the analysis of relative intake rates if no fish attempted to eat them before they had fallen to the floor of the tank (as this indicated that there was little competition for them). The experimental trials were run in such a way that each pair experienced each of the group sizes only once and thus the number of replicates (r) for each group size is: group size two, $r = 8$; group size four, $r = 4$; group size eight, $r = 2$; and group size 16, $r = 1$. All quoted probabilities for statistical tests are for two-tailed tests of significance.

Results

There was no significant growth in the fish over the experimental period (paired t-test, Standard length: $t = 0.39$, $df = 15$, $p = 0.70$; wet weight: $t = 1.10$, $df = 15$, $p = 0.29$). This indicates that any potential changes in relative competitive ability between fish could not have been due to changes in their relative sizes over the

experimental period, which has been previously shown to have a strong effect on competitive ability (Gill & Hart 1996).

A measure of relative competitive ability was calculated for each pair of fish at each of the four group sizes. To do this we defined the individual in each dyad which was most successful in the two fish trial (or the next group size if the intakes were equal) as the ‘good’ competitor of that pair. Next, a percentage value (‘percentage won’) was calculated for each pair at each of the four group sizes investigated. This was done by taking the intake (at the group size in question) of the ‘good’ individual in the pair and dividing it by the total number of pellets out of 70 consumed by the pair in the group size trial in question. This value was then multiplied by 100 to give the ‘percentage won’ measure of relative competitive ability. We decided to use percentage won values in the analyses as we feel that these values are a more accurate reflection of the data, due to the loss of values inherent in the use of ratios of intakes where the denominator is zero. Figure 2.2 shows the mean percentage won value for each group size and indicates that there appears to be no real differences in the values across the different group size trials (Repeated measures ANOVA, Univariate test: $F_{3,21} = 0.407$, $p = 0.750$).

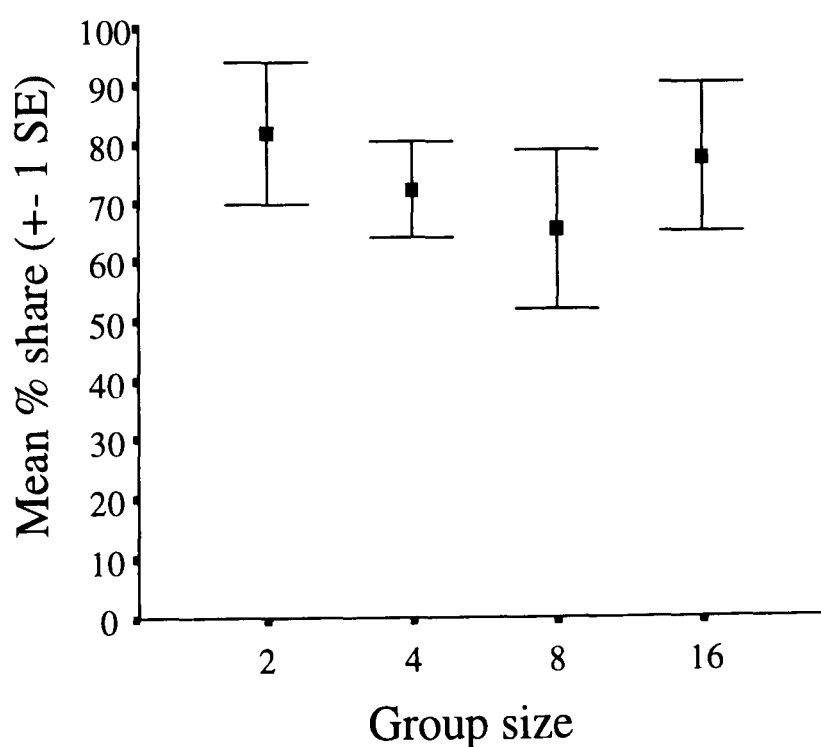


Figure 2.2. Mean (\pm SE) percentage of pellets won by the initially better competitors against group size ($n = 8$ dyads for all points). Repeated measures ANOVA indicates no significant differences between the group sizes (analyses were performed on arcsine-transformed data).

In order to check that satiation was not confounding other factors in the analysis we carried out a Wilcoxon Signed Ranks test on the percentage won data for the first and second 35 pellets for the trials. All trials of each group size were considered together, with each pair as a data point. We found no significant differences between the percentage won by the better competitor in each pair in the first and second halves of the trials (group size 16, $n = 8$, $Z = -0.412$, $p = 0.680$; group size 8, $n = 8$, $Z = -1.461$, $p = 0.144$; group size 4, $n = 8$, $Z = -1.439$, $p = 0.150$; group size 2, $n = 8$, $Z = -0.962$, $p = 0.336$). The data in the above tests were modified slightly from that used for other analyses in that, in cases where neither fish in a pair fed, the percentage won value was taken as zero. It was decided that, in terms of the differences in the distribution of resources, a situation where neither fish in a pair obtained any food was analogous to one where the individual defined as 'good' (see above) obtained no food, whilst the other individual in the pair did obtain food. Thus, in both cases when calculating the ratio, the denominator was zero. The results of the tests indicate that satiation was not influencing the results.

Repeated measures ANOVA was used to analyse the data on relative food intake of the two fish in a dyad across the range of group sizes, with relative body size (ratio of standard length (SL) of the individuals in each pair) included as a covariate. We found no significant effect of group size upon relative competitive ability (Univariate test: $F_{3,18} = 3.103$, $p = 0.053$). The significant interaction term ($F_{3,18} = 3.263$, $p = 0.046$) indicates that any effect of group size upon relative competitive ability is dependent upon the difference in body size between the two fish in question. Furthermore, non-significant between-subjects effects ($F_{1,6} = 0.028$, $p = 0.872$) indicate that there is no direct effect of differences in body size between the two fish on relative competitive ability.

In order to investigate further the effects of the difference in body size between individuals within a pair, we regressed the measure of relative competitive ability (percentage won value) on group size for each pair and then used this regression slope as a summary of each pair's interactions. We then plotted these summary values against the SL ratios of the experimental pairs (figure 2.3). It can be seen that

as the size disparity of the pairs increases the summary slopes change sign from negative to positive. Thus, the food intake of fish of similar size converges as group size increases, whereas that of dissimilar sized fish diverges ($r^2 = 0.51$, $n = 8$ dyads, $p = 0.045$) and this effect remains significant even with the removal of the two most extreme points ($r^2 = 0.69$, $n = 6$ dyads, $p = 0.041$). Thus, although there appears to be no overall effect of group size on relative competitive ability (see earlier result of repeated measures ANOVA on the overall effect of group size) there is, in fact, quite a complicated effect with opposite trends occurring, dependent upon differences in the size disparity of the pairs.

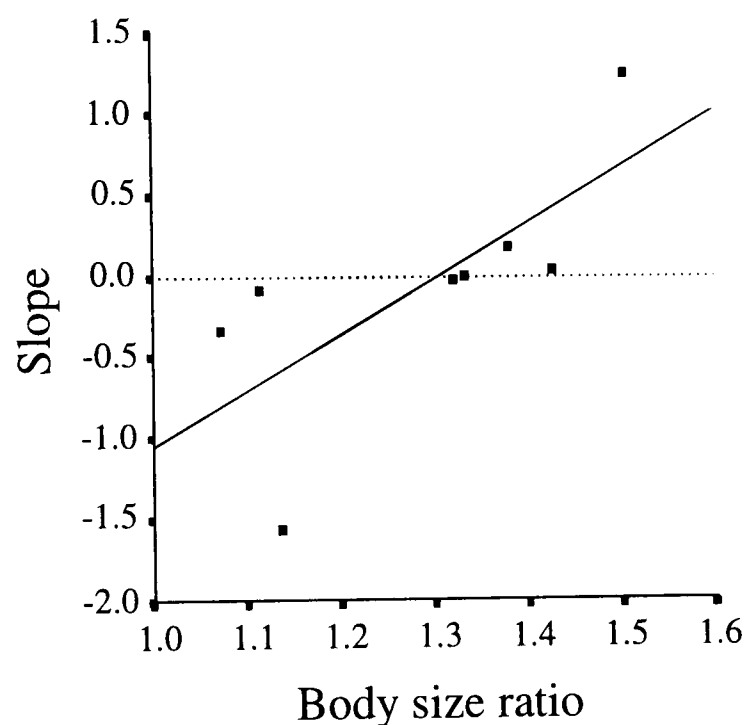


Figure 2.3. Slopes for the regressions of percentage won on group size, plotted against disparity in body size of the experimental pairs.

Discussion

Our results suggest that the effect of group size upon relative competitive ability, in minnows at least, will be dependent upon the relative body sizes of the individuals involved. Although the trend for dissimilarly-sized fish is similar to that of Sutherland and Parker's phenotype scales intercept model, we cannot explain the trend for similarly-sized fish using either of their phenotype models. To try and explain our results we have developed a conceptual model relating a competitor's intake to the size of the group in which it is competing as well as its 'rank' within

that group. 'Rank' can be considered as ranked size or competitive ability within the group, or some other function of body size. Considering this model, a pair of fish foraging on their own will clearly be ranks one and two, but if group size is increased by the addition of randomly sized competitors then we can see that the ranks of the original pair are increasingly unlikely to be those at the top. It is this basic concept that we use to explain our experimental findings.

If we first take a curve that describes the intake of a set of competitors at a certain group size in relation to their rank in the group, we can then plot a series of these curves corresponding to a range of group sizes (figure 2.4). If we now consider a high-ranking or relatively large pair of fish with similar SLs we can see that as group size increases the pair will tend to stay at, or near, the top of the rank order: i.e. although they will move down to a different slope when group size increases, they will not move position in the rank order. As these fish move down to different group size slopes their absolute intakes will decrease but the ratio of lower divided by higher intake will increase as their absolute intakes become more similar. Next we can consider another pair of fish with similar SLs, but this time with a small absolute size or low rank: as group size increases these fish are likely to be 'pushed' down the rank order as well as moving onto different group size slopes as the number of competitors increases. However, as their absolute intakes decrease the ratio of their intakes will increase, as with the high ranked fish. Finally, a pair with a large disparity in SLs or rank will be more likely to become separated from each other on the ranking scale as group size increases, in that new competitors are more likely to be of a rank or size intermediate to the two members of the original pair. Thus, the rank orders of these two fish are more likely to separate as group size increases leading to a decrease in the ratio of their intakes and their absolute intakes becoming less similar.

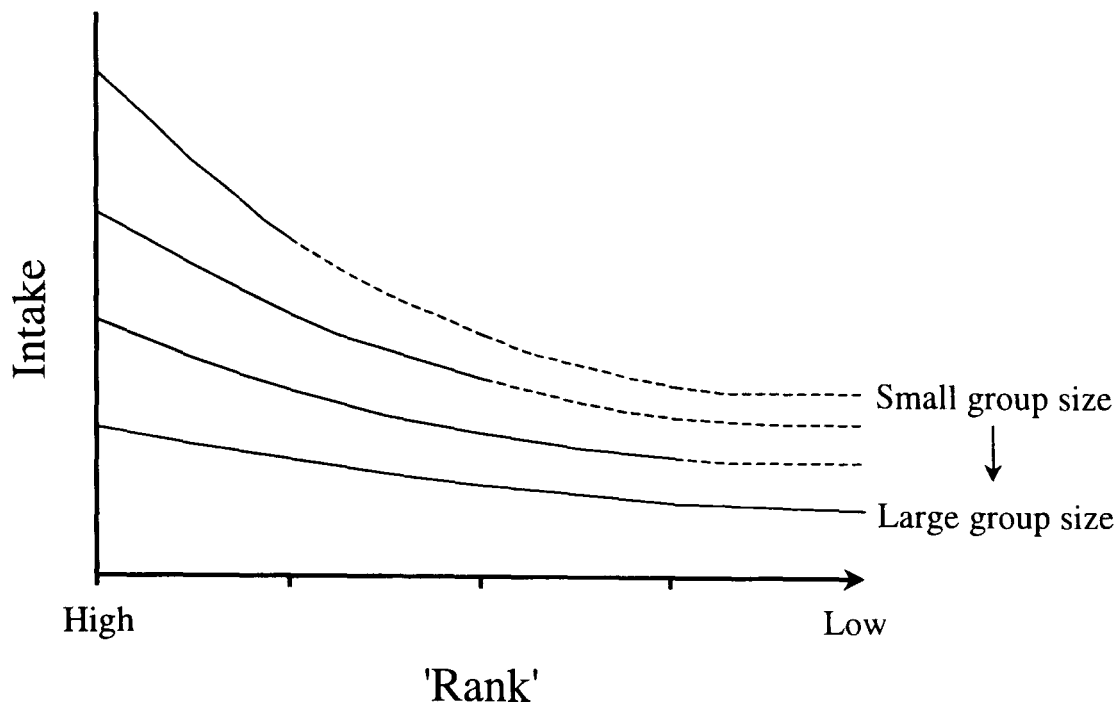


Figure 2.4. Plot of the conceptual model developed to explain the results. Each curve represents the intakes of a set of competitors at a certain group size. We suggest that there is a general decrease in intake with group size and that the slopes become flatter indicating more similar intakes at higher densities.

If we take this model and make the assumption that our rank scale approximates to Sutherland and Parker's different phenotypes, then we can plot slopes for the intake of different ranks (phenotypes) against group size. Transformation by taking logs of both axes allows us to compare our model (figure 2.5a) with plots from Sutherland and Parker's phenotype scales intercept model (figure 2.5b). Although superficially similar to Sutherland and Parker's model, ours suggests that the relationship between rank (phenotype) and group size is not a constant one. The change in steepness of the slope as group size increases is suggestive of a situation where differences in relative competitive ability become rapidly less pronounced as group size increases and for some situations, this may be a more appropriate prediction than that of the phenotype scales intercept model.

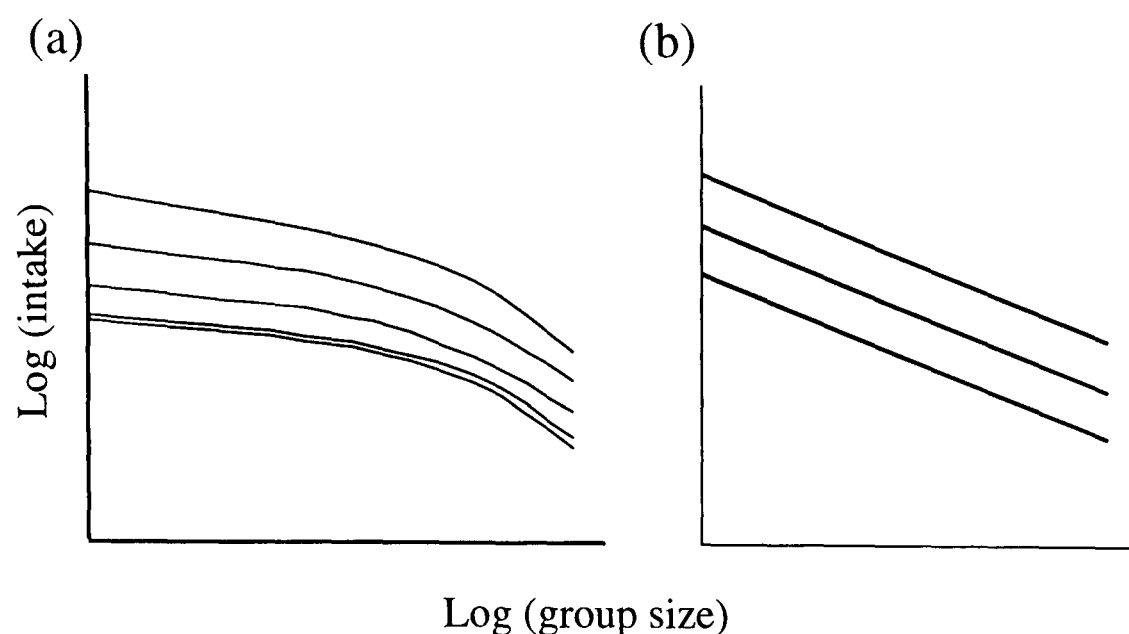


Figure 2.5. (a) Log transformed plot of the conceptual model with group size on the x axis and 'rank' plotted as slopes. Comparison with the Sutherland and Parker's phenotype scales intercept model (b) shows some important differences in the shape of the plotted slopes.

Tregenza *et al.* (1996) suggest that in similar continuous input situations there was an effect of competitor density on relative competitive ability and initially this seems to agree with our findings for pairs of fish of a similar size, although they give no details on size disparity. However, they suggest that this finding may be a result of competition switching from a contest between individuals at low density to scramble competition at higher ones. We feel that this switching from one type of interaction to another is probably due to their experimental set-up utilising what is in effect a defensible point source of food input compared to the more dispersed, although still discrete, patch created by our feeder. The use of a single stream of water to deliver the food items may at first appear to represent a semi-natural situation but, unlike the spreader apparatus used in our experiments, this set-up would produce a patch of relatively small dimensions (almost a point-source) which can be easily defended (at least at smaller group sizes) by one fish. This system could account for observed decreases in the most dominant individual's intake with increasing density (Inman 1990, Tregenza *et al.* 1996). Monaghan and Metcalfe (1985) report comparable behaviour in European hares (*Lepus europaeus*) and Rubenstein (1981), working with the Everglades Pygmy Sunfish (*Elassoma evergladei*), found a similar change whereby the type of competition changed from territorial defence when resources

were clumped to more general competition when resources were dispersed randomly, at both high and low population densities.

Although we attempted to minimise the effect of memory (Milinski 1979, 1984) of other individuals in our experiments by maintaining experimental pairs separately and by the temporal sequence of the trials, this phenomenon could still influence our results in terms of learning how the trials 'worked'. We feel that the training sessions conducted before the main trials should mean that the fish could gain little extra information on the trials themselves and hence could not significantly affect the results. In addition, in Milinski's (1979, 1984) experiments with three-spined sticklebacks (*Gasterosteus aculeatus*) the effect of memory was primarily in terms of preference for one end of the tank or the other, whereas in this experiment only one feeding patch was available per trial.

In conclusion, we can say that the effect of group size on relative competitive ability in continuous input situations can be variable, and dependent upon the context and specific circumstances of the interactions. Although we found no effect of group size upon relative competitive ability, it appears that there are actually two processes that act to cancel each other out. These effects are dependent upon the difference in body size between the two fish in a pair, but this difference itself has no overall effect on relative competitive ability. The two effects act so that intake rates of similarly sized fish converge as group size increases, whilst those of dissimilar sized fish tend to diverge.

These results add to the growing list of factors which can potentially decrease the fit of empirical data to the classical ideal free distribution models - when competitors move from one patch to another they will change the group size around that patch and thus potentially change the relative competitive ability of all competitors both on that patch and within the whole habitat.

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**GROUP SIZE AND RELATIVE COMPETITIVE ABILITY: GEOMETRIC
PROGRESSIONS AS A CONCEPTUAL TOOL**

Abstract

Contrary to the assumptions of many previous theoretical models, group size has recently been shown in experiments to have an effect on the relative (as well as absolute) competitive abilities of group members. Here we introduce a novel and effective mathematical tool for describing how relative competitive ability will change for any two specified individuals within a group as group size changes. We show that there is no simple general rule for describing how relative competitive ability will change with group size. A subsequent empirical test of the model helps illustrate that very specific knowledge of the system under study is needed in order to produce robust predictions.

Introduction

It is commonly observed in nature that, where individuals compete for a divisible resource, their shares of that resource are unequal (eg. matings on a lek: Davies 1978, Mackenzie *et al.* 1995; males competing for arriving females: Parker 1970; or fish waiting for drifting prey in a stream: Milinski 1979). Clearly we would like to know how the relative rewards to individuals (often called their relative competitive ability) vary under different ecological conditions. The ecological variable that has recently come under scrutiny is that of group size. Many classical models have assumed that the relative competitive ability of two specific individuals is independent of the size of the group that they interact within. A few models, such as modifications of the ideal free distribution (IFD, Fretwell & Lucas 1970), have incorporated the idea that the relative ability of individuals to compete for resources may vary according to characteristics of the patch (e.g. Sutherland & Parker 1985, 1992, Parker & Sutherland 1986, van der Meer 1997). There is also limited empirical evidence for changes in relative competitive ability between resource patches (Sutherland *et al.* 1988, Grand 1997), although in some cases changes in the type of competition occurring between patches has been implicated (e.g. Inman 1990, Tregenza *et al.* 1996). Similar changes in the way individuals interact were found by Gillis and Kramer (1987) who showed that density-related reductions in foraging efficiency could reduce the fit of distributions of foraging zebrafish (*Brachydanio rerio*) to the IFD. Recently the general assumption of constant relative competitive ability across group sizes has been found to poorly describe the results of some experiments (Tregenza *et al.* 1996, Humphries *et al.* 1999). In particular, Humphries *et al.* (1999) found that individuals of similar competitive ability tend to become more similar in ability as group size increases whereas individuals of widely differing competitive abilities tend to become even more different as group size increases. Humphries *et al.* (1999) introduced a graphical model to attempt to explain these results and here we produce a quantitative model to explore both the validity and generality of the mechanisms described by Humphries *et al.*. Whilst the graphical model of Humphries *et al.* is plausible its lack of quantitative predictions makes it hard to test and leave its generality unclear. It is to solve these two problems that we develop a more rigorous model. Furthermore, we present an effective quantitative methodology for describing how relative competitive ability

changes with group size and the consequences of this, both for individuals and for larger structures (groups).

The graphical model on which Humphries *et al.* (1999) based their arguments implicitly assumed that there was a stable ranking of individuals, and that the reward obtained by an individual declined with reducing rank and with group size. The first of these assumptions is well supported by the literature, as indeed are the second and third (e.g. Coates 1980, Ens & Goss-Custard 1984, Milinski 1984, Tregenza *et al.* 1996, and references in Tregenza & Thompson 1998). In addition, the absolute decrease in gain between consecutive individuals decreased with the absolute ability of the two individuals concerned and the detrimental effect of group size on gain had a greater effect on those individuals of higher rank (i.e. better competitors). However, in order to develop a quantitative model we need to specify the exact form of the distribution of gains. Drawing on recent work by Kokko and Lindström (1997) and Kokko *et al.* (1998) on lekking behaviour, we adopt a declining geometric distribution to describe the distribution of gains within the group. The geometric distribution has the attraction of simplicity in that the shape of the distribution is described by a single parameter. However, this simplicity is bought at a cost in biological realism since an implicit assumption of the geometric distribution is that the relative competitive ability of each individual in the ranking is the same fixed fraction of that proceeding it. We can think of no biological mechanism which justifies such an assumption, however, Kokko *et al.* (1998) fitted geometric distributions to data from all 71 leks in their study. Further, they found that the estimated skew parameter showed a general decline with increasing group size, which supports the last of the assumptions of Humphries *et al.* (1999). Additional support comes from a basic tenet of the IFD, that as competitor density increases the average gain within a patch with continuous input decreases as resources are shared between more individuals. Hence, it would appear that the geometric distribution with a skew parameter that is a declining function of group size could be an effective descriptive model of the relative gain of individuals within a competitive group. In the rest of this paper we show that such a descriptive model does provide a good description of relative competitive ability in a competitive situation analogous to that of Humphries *et al.* (1999). We then use the model to provide a clear quantitative

explanation of the results of Humphries *et al.* and subsequently use this tool as a vehicle to seek a qualitative understanding of the consequences of changing group size for relative competitive abilities.

Theory of the relationship between group size and relative competitive ability

We assume that the intake rates $Q_{(i, N)}$ of individuals of rank i (where increasing i represents decreasing competitive ability) in a foraging group of size N can be represented by a decreasing geometric series,

$$Q_{(i, N)} = \frac{C\lambda(1-\lambda)^{i-1}}{1-(1-\lambda)^N} \quad (1)$$

Where C is a constant (the total intake rate of the whole group) and $\lambda \in (0,1)$ is the skew, which for the moment we assume is a constant independent of group size, and which describes the distribution of intakes across the group. The greater the skew, the more rapidly intake declines with increasing rank i .

Let us consider that in a group of any size, individual x always occupies a better rank than individual y such that $y = x + z$, where $1 \leq z \leq N-1$. The ratio of the poorer competitor's intake rate to that of the better competitor $r_{(x,y)}$ is given by

$$r_{(x,y)} = \frac{Q_{(y,N)}}{Q_{(x,N)}} = (1-\lambda)^{y-x} \quad (2)$$

This model predicts that the greater the skew (λ), the greater the difference in relative competitive ability of two individuals of fixed ranks: i.e. the smaller $r_{(x,y)}$. Similarly, the greater the rank difference between two individuals (the bigger $y-x$ is) the greater the difference in relative competitive abilities and so the smaller $r_{(x,y)}$. For fixed ranks x and y , we see that the group size N has no effect on relative competitive ability. This is a direct result of our simple assumption that the slope of the geometric progression (described by λ) is independent of N , which we now relax.

We now assume that skew declines with increasing group size. Specifically, this decline is described by the parameter b (where $b > 0$) such that

$$\lambda(N) = \frac{\lambda_2}{(N-1)^b} \quad (3)$$

where λ_2 is the value of λ in a group size of two individuals - the smallest group size for which λ is meaningful. If λ is a function of N as in equation (3) then substituting this into (2) gives

$$r_{(x,y)} = \left(1 - \frac{\lambda_2}{(N-1)^b} \right)^{y-x} \quad (4a)$$

This equation allows us to make predictions about the change in relative competitive abilities (i.e. the relative proportions of the total resources obtained by the group) of individuals x and y in groups of two different sizes by generating the ratio of $r_{(x,y)}$ for the larger group size divided by that for the smaller group size. We denote this ratio of ratios $r'_{(x,y)}$. Values of $r'_{(x,y)}$ less than one indicate intakes of the two competitors becoming less similar with increasing group size, whilst those greater than one show that the intakes become more similar as group size increases.

In order to understand more generally the model predictions we need to be able to predict how $r_{(x,y)}$ changes as N increases. Further examination of equation (4a) indicates an interesting aspect of the model in this respect. If equation (4a) is rearranged thus,

$$r_{(x,y)} = \exp \left((y-x) \ln \left(1 - \frac{\lambda_2}{(N-1)^b} \right) \right) \quad (4b)$$

then it is easy to study the predictions of the model for a maximally dissimilar pair as group size becomes very large (i.e. as N and $(y-x) \rightarrow \infty$). Specifically we find that the value of $r_{(x,y)}$ in this limit depends on the value of b . There are three cases:

- 1) $0 < b < 1 \Rightarrow r_{(x,y)} \rightarrow 0$
- 2) $b = 1 \Rightarrow r_{(x,y)} \rightarrow \exp(-\lambda_2)$
- 3) $b > 1 \Rightarrow r_{(x,y)} \rightarrow 1$

Small changes in the value of b , which may have little effect on $r_{(x,y)}$ when N is small, can produce dramatically different predictions for $r_{(x,y)}$ when N is large. Figure 3.1 illustrates the trends for $r_{(x,y)}$ for some representative values of the parameters N , λ_2 and b using equation (4). The plots show values of $r_{(x,y)}$ for maximally dissimilar ranks ($x = 1$ and $y = N$) at each N . It can be seen that even slight changes in the parameters λ_2 and b can have marked effects on the relationship between the intakes of individuals x and y with increasing group size. It is difficult to predict whether $r_{(x,y)}$ will increase or decrease with increasing group size when $(y-x)$ is large without very precise knowledge of the value of b . In addition, because of the difficulty in assessing the success of lower-ranking individuals due to their low rate of resource acquisition, it can be difficult to ascertain λ experimentally, which can further compound the problem of the model's sensitivity to b . In spite of this, the required accuracy of any estimation of b can be defined to some extent by consideration of equation (4b). For values of b other than those close to one, relatively large variation between the estimation and the true value will produce the same result: $r_{(x,y)}$ will tend to either one or zero. However, for values of b close to one, even small changes in the value of this parameter can drastically alter model predictions. Lastly, notice from figure 3.1 that one cannot safely assume that an initial upward trend in $r_{(x,y)}$ with N will inevitably continue as N is increased further (see $b = 0.75$ in figure 3.1).

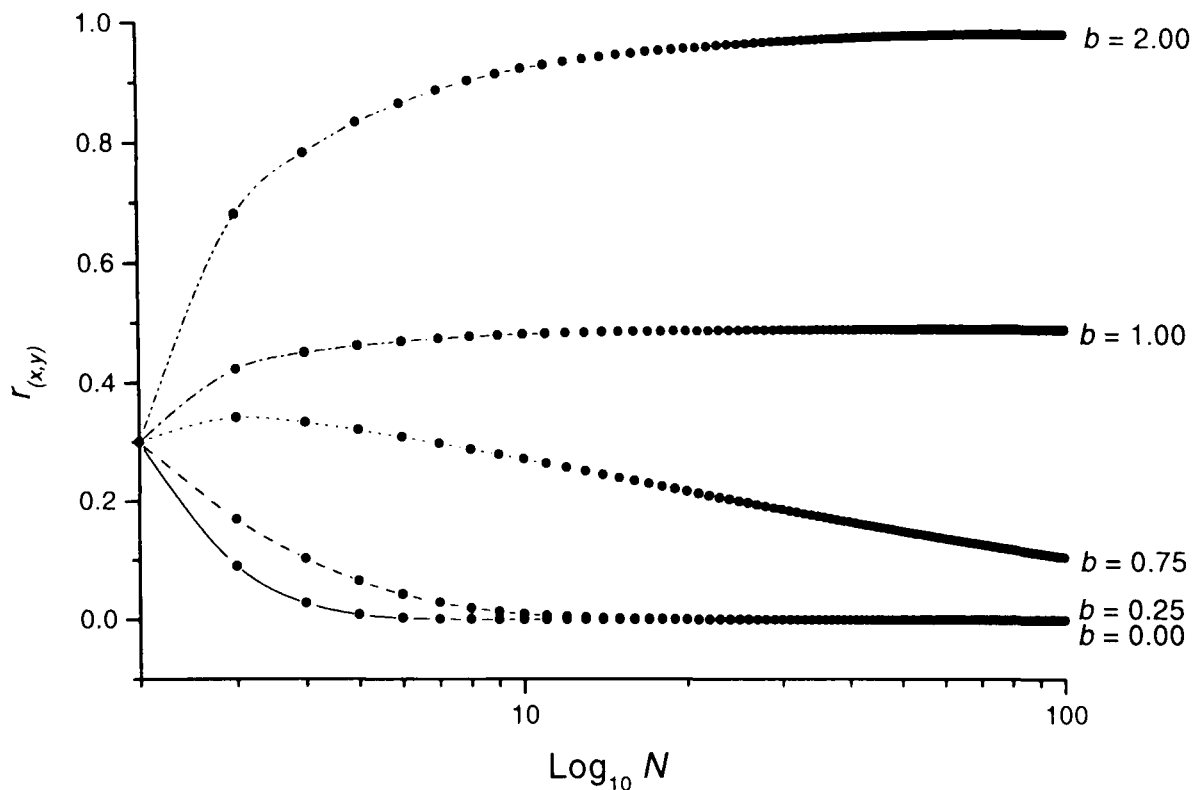


Figure 3.1. Predicted changes in the relative competitive ability of the best and worst competitors in a group ($x = 1$ and $y = N$) against changing group size ($N = 2$ to 100), based on equation (4). λ_2 is taken to be 0.7 . Note that $b = 1.00$ tends to $\exp(-\lambda_2)$, i.e. 0.496 .

Experimental methodology

In order to test the predictions generated by this model we used three-spine Sticklebacks (*Gasterosteus aculeatus*) collected from the River Endrick, Stirlingshire, Scotland. Nine groups of ten fish were kept in separate plastic stock tanks measuring $334 \times 180 \times 225$ mm (L \times H \times W), under a light and temperature regime of 10:14 (L:D) and $10 \pm 1^\circ\text{C}$, throughout the experiment. They were fed to satiation daily with frozen Chironomid larvae except during feeding trials (see below).

Individual fish were marked with two 1-2mm lengths of thin plastic insulation sleeving from electrical wire in different combinations of colours (excluding red which tends to elicit attempts by other fish to feed on the tag (pers. obs.)). The sleeves were pushed gently onto the first and second dorsal spines of the fish and secured with a small spot of rapidly curing adhesive. In light of the strong linear relationship between length and wet weight in three-spine sticklebacks (Krause *et al.* 1998) wet weights were measured, in order to reduce the amount of stress the test fish were subjected to.

The rank orders of food intake within each group of ten fish were used as a measure of relative competitive ability. The rankings were obtained as follows. Each group of fish was deprived of food for one day to increase and standardise the feeding motivation of the fish. Next, the groups of ten fish were transferred to an arena tank (610 × 307 × 295 mm) with opaque sides and a mesh floor raised 15mm from the base of the tank. The mesh floor allowed us to ensure that any food items not consumed in the water column were unavailable to the fish during the rest of the trial. The fish were allowed to acclimatise for 30 minutes, then 40 Chironomid larvae of between 12 and 14mm in length were introduced singly to the tank via a pipette (only adding the next item once the previous one had been completely consumed or had fallen through the mesh floor of the tank). Food items were added in a random manner within a discrete area of approximately one third of the surface area of the tank. Thus, the food input was random with respect to the distribution of individuals in the tank, and although the groups tended to congregate in the feeding area no individual fish could defend the input site. As food items were added the identity of each fish consuming an item was noted. This procedure (one day of fasting followed by a trial day) was repeated sequentially four times for each group and a ranking based on mean intake was obtained for each individual, with the fish obtaining the most bloodworms being ranked one and the individual obtaining the least being ranked ten. After each trial the fish were fed to satiation with frozen Chironomid larvae in order to standardise their nutritional state.

We tested for the repeatability of the individual trial intakes at group size ten using Kendall's coefficient of concordance (W). This was significant for all groups (lowest coefficient: $W = 0.524$, $P = 0.026$), indicating a significant agreement in the rankings between trials. The mean rank generated for each individual using the above test was later used as that individual's rank within its group. These rankings were used to derive pairs of fish (22 in total) whose mean ranks were either 'similar' (within three ranks of each other) or 'dissimilar' (more than four ranks apart). Each pair was made up of two fish selected from the same group of ten individuals. The relative intakes of the two members of each dyad were then measured in a group size of two using the same arena tank and a similar protocol as before, but this time using only one

dyad in the arena tank at any one time and introducing only 20 food items. Again, four repeats were carried out for each dyad.

In order to analyse the results for each of the dyad trials we divided the intake of the lower ranked individual in a dyad (based on the ranks from the original ten fish experiments) by the intake of the higher ranked individual to obtain an intake ratio ($r_{(x,y)}$). We then took a mean of the four ratios generated by the four repeats for each dyad, and divided the mean ratio for each dyad at group size ten by those for the trials carried out at a group size of two. The resulting value represents the change in relative competitive success ($r'_{(x,y)}$) with an increase in group size from two to ten.

In the experiments, groups of ten fish received 40 food items, whereas dyads received 20 items. It could be argued that maintaining an equal number of food items per fish across trials of different group sizes would more accurately reflect relative competitive success. However, there then exists the strong possibility of problems in accurately determining the relationship between fish where one individual is able to obtain a large proportion of the food items if few items are available at smaller group sizes. Counteracting this by increasing the number of food items available in the smaller trials would also necessitate an increase in food available in the larger group size trial, leading to problems with satiation of better competitors. We therefore carried out all of our analyses both on the full data sets and on just the first eight items of the original 20 in the dyad trials. However, as both data sets gave similar results we present only those for the original full data set here.

Results

Mean wet weight (\pm s.d.) for the 90 fish was 0.56 ± 0.17 g and the maximum difference in weight between individuals in a shoal of ten fish (mean of nine groups) was 0.50 ± 0.15 g. We found no relationship between an individual's size (wet weight) and its competitive ability in the groups of ten individuals ($r_p = 0.192$, $n = 90$, $p = 0.070$) nor between the difference in size between individuals in a dyad and the difference in their ranks from the trials at a group size of ten ($r_p = 0.067$, $n = 22$, $p = 0.768$).

We first investigated the appropriateness of a geometric series as a description of our relative competitive ability data by estimating a mean λ value from the data on intake rates for each of the two group sizes used. For the group size of ten fish we fitted a model of the form

$$P_i = ad^{(R_i-1)} \quad (5)$$

where P_i is the proportion of food items consumed by an individual of rank R_i ,

$$d \equiv (1 - \lambda), \quad (6)$$

and

$$a \equiv \frac{\lambda}{1 - (1 - \lambda)^N}. \quad (7)$$

This meant that a simple linear regression of R_i on $\log(P_i)$ could be used to find the parameters a and d thus,

$$\log(P_i) = \log(a) - \log(d) + R_i \log(d) \quad (8)$$

and we were able to calculate λ from d and then calculate a . We tested the accuracy of our estimated λ values by comparing the value of a calculated from equation (8) (a_{regr}) with that from equation (7) (a_{calc}). As a_{regr} was within the range of $a_{\text{calc}} \pm \text{s.e.}$ (calculated by substitution of the s.e. of the slope for λ in equation (7)), we judged our estimate of λ to be an accurate one, and the intakes to be geometrically distributed.

To calculate λ for the dyads (i.e. λ_2) we used equations (5) and (6). Thus, when the two individuals are ranks one and two,

$$\frac{P_1}{P_2} = \frac{1}{(1 - \lambda_2)} \quad (9)$$

and therefore,

$$\lambda_2 = \frac{P_1 - P_2}{P_1} \quad (10)$$

The values of λ obtained by these methods were smaller at the larger group size ($\lambda_{10} = 0.229 \pm 0.031$ (s.e.)) than at the smaller one ($\lambda_2 = 0.340$).

In order to further check the accuracy of our λ values in describing the data we generated an expected distribution of mean intake rates for each rank using our calculated λ_{10} value and equation (1), and tested the fit of the data to the expected distribution using the Kolmogorov-Smirnov goodness of fit test for discrete data (Zar 1996). There was no significant difference between the data and the expected distribution (original $(d_{max})_{10, 40} = 2.611$, $P > 0.50$), indicating that this specific geometric series is a good fit to the data.

Next we tested the measured data against the model predictions. Since λ was not constant across both group sizes, we used equation (4) to generate the r' values. We calculated b , the measure of change in skew, by rearrangement of equation (3). By applying the calculated values for λ_2 and b to equation (4), as well as the distances between rank and group size N we were able to generate model predictions to test against the measured data. These predictions were in the form of $r'_{(x,y)}$ values generated from the $r_{(x,y)}$ values produced by equation (4). Wilcoxon's signed rank test (two-tailed) indicated that there was no difference between r' values generated by the model and those generated from the data ($Z = -0.211$, $n = 22$, $P = 0.833$) and Spearman's rank correlation gave highly significant negative correlations between r' and rank distance for both the data and the model predictions (data $r_s = -0.625$, $n = 22$, $P = 0.002$; model $r_s = -1.000$, $n = 22$, $P < 0.001$).

Figure 3.2 illustrates the plots of rank distance against the r' values from the data and those generated from our model of equation (4). The figure indicates that the original predictions of the conceptual model of Humphries *et al.* (1999) are upheld, i.e. that pairs of dissimilar competitive ability tend to have r' values of less than one whilst those of pairs of similar competitors tend to be greater than one. The large variance seen in the data when the two individuals are very similar in ability ($(y-x)$ is small) is likely to be due to stochastic variation, as when intakes are very similar small fluctuations will have a strong influence on the final results.

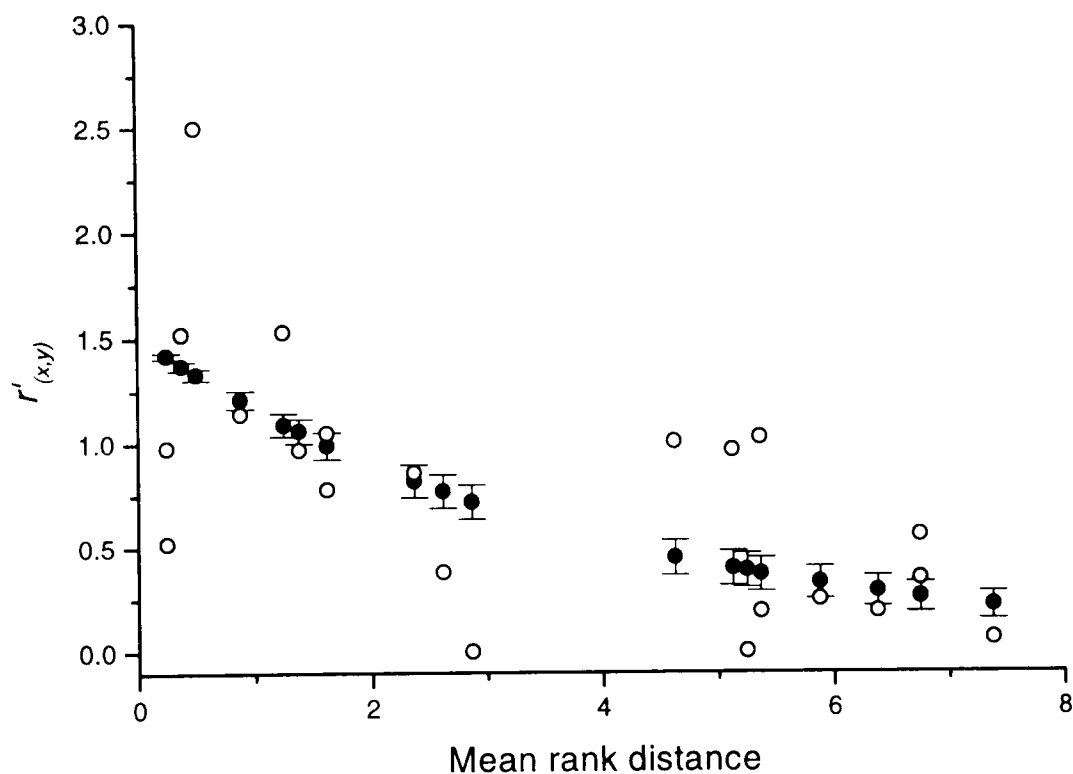


Figure 3.2. Plot of $r'_{(x,y)}$ (the change in relative competitive success with increased group size) against the difference in competitive rank of a pair of fish for the stickleback data (open circles) and the model (equation (4), filled circles). Error bars indicate the model predictions using the maximum and minimum b values generated by using $\lambda_{10} \pm \text{s.e.}$

Discussion

This work shows that a geometric progression gives a good fit to ranked intake (a measure of relative competitive ability) at a given group size for three-spine sticklebacks and that this measure of intake skew is not constant, but rather changes with group size. The change in skew with group size is described by the parameter b , which allows us to mathematically describe the effects of changing skew on relative competitive ability. Hierarchies of competitive ability are commonly observed in

both field and laboratory experiments (see references in Tregenza & Thompson 1998), and so geometric progressions may be a useful method of describing relative competitive abilities between individuals in a wide variety of situations.

Due to the unavoidable sequence of the feeding trials (four repeated trials with ten fish followed by a further four repeats with dyads) in our experiment, there exists the possibility that learning effects may have influenced our results. For instance, the individuals used in the dyadic trials experienced the trial procedure eight times whilst some individuals only experienced it four times. Learning effects have previously been shown to be an important factor when using three-spine sticklebacks in experiments with varying patch qualities (Milinski 1994) and it is possible that the same phenomenon could occur with group size in this study. However, we feel that such an effect is unlikely to be important here, due to the random way in which the food items were introduced to the arena tank (see above) and because all experimental fish had been fed in a similar way, using a pipette, during their entire life in captivity.

The fit of our data from our study on foraging and Kokko *et al.*'s (1998) on leks suggests that geometric progressions may well have applications in other areas of resource acquisition. However, the lack of a biological mechanism by which to explain the assumption of proportional differences between ranks would merit further investigation, as would situations where the difference between ranks is not necessarily as inflexible as that described by a geometric progression.

The importance of hierarchical competitive abilities in many situations where groups compete for resources suggests that our model could have wide applications in many areas. Possible effects of group size in many studies are often ignored, but this work offers a method of describing changes in group size and its effect on resource acquisition in a variety of situations. However, application of this work to such situations may not be as straightforward as it appears. Although we are able to make accurate predictions about changes in relative competitive abilities as a function of group size for our experimental conditions, it is likely that changes in b will markedly alter model predictions for other systems, even to the extent that the

predictions are reversed when considering small as opposed to large N (fig. 3.1). However, it is important to note that the major effect of small changes in b will be apparent when $(y-x)$ tends to $(N-1)$, that is, when considering pairs with maximally dissimilar ranks. Nonetheless, as discussed above, we can offer a guide to the required accuracy of an estimation of b . This should help to indicate whether changes in b observed in a particular situation will greatly alter the predictions for relative competitive ability in that situation.

Kokko *et al.* (1998) drew similar conclusions to ours for mating success of individuals on leks. They suggested that small, and possibly statistically non-significant, changes in the way mating skew responds to lek size, together with changes of a similar magnitude in the mating distribution itself, could produce very different predictions concerning optimal lek sizes for individual males. The similarity of these two situations suggests that there will be similar effects on individual optima in other situations.

The effects of competitor density on relative competitive ability we describe are likely to be important in shaping group sizes for many foraging animals. In cases where the model predictions are the same as the conceptual model of Humphries *et al.* (1999), it will pay individuals to associate with other individuals who are at best equal in competitive ability, and preferably with ones which are poorer competitors. A preference of this type has been found in minnows by Metcalfe and Thompson (1995). If size and relative competitive ability are related then this idea should also apply to size segregation. Foraging differences have already been put forward as explanations of size segregative shoaling (e.g. Pitcher *et al.* 1986, Peuhkuri 1997) but when considered with our findings some results of experiments investigating foraging activity in relation to oddity (e.g. Peuhkuri 1997, 1998) may now provide more support for relative competitive ability as an important factor in shoal composition. The theoretically optimal group size for any individual is unlikely to be met in most situations (Sibly 1983, Clark & Mangel 1984, Pulliam & Caraco 1984, Ranta 1993) and animals may be expected to form groups of a size that depends on group entry rules (Giraldeau & Caraco 1993). Considering our results, we suggest that in mixed competitive ability shoals there will be trade-offs within the group not

only in terms of group size, but also in terms of group composition. Therefore, we suggest that future theoretical work should consider not only group size and structure, but also how quickly an individual's payoff deteriorates with perturbation away from their individual view of optimum size and composition. As a result it should be possible to determine how an individual's tolerance for deviations from a perceived optimum affects its decision to leave or join a foraging group.

In conclusion we propose that, contrary to the current paradigm, there is no general rule describing how relative competitive ability will change with group size. Rather, we propose a novel and effective tool for describing how relative competitive ability will change with group size for any two specific individuals based around a geometric progression of intakes. However, to use this tool for a particular system one must have specific knowledge of that system, and in particular an accurate value for the way in which intake skew changes with group size.

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**PATCH CHOICE AND RISK: RELATIVE COMPETITIVE ABILITY IS
CONTEXT DEPENDENT**

Abstract

The relative abilities of individual cichlids (*Tilapia zillii*) to obtain food under scramble competition was highly repeatable between trials utilising a single input source, regardless of whether the input was constant or variable. However, when given a choice between two patches differing only in their temporal variability in input about an identical mean, an individual's rank based on intake in one patch was uncorrelated with either its intake in the other patch or its intake in the single-patch trials. In the two-patch trials, certain individuals both spent more time in food patches and visited patches more often than others, and overall the fish spent more time in the constant rate patch than the variable patch, leading to more items being consumed from the constant rate patch. Causes and consequences of this dependence of relative competitive ability on the context of the foraging situation are discussed.

Introduction

Relative competitive ability is a concept frequently applied to studies in behavioural ecology, and is generally defined as the ability of an individual to compete for resources in relation to the abilities of others within a group. In addition to the obvious applications to dominance interactions and resultant hierarchies, relative competitive ability is commonly considered in the context of the ideal free distribution (IFD, Fretwell & Lucas 1970, Fretwell 1972), which is commonly used to explain the distributions of animals in a heterogeneous environment. In its simplest form, the IFD predicts that animals of equal competitive ability which are 'free' to travel anywhere in their environment without costs and 'ideal' in that they have complete knowledge of their environment, will exploit those patches where they are able to maximise their resource gain. In an environment with more than one resource patch, density-dependent effects will lead to an equilibrium at which all patches provide an equal resource acquisition rate and consequently no individual will gain by moving to another patch. However, assumptions of the IFD are frequently violated in the natural world, and many modifications have been put forward to try and increase the realism of the model. Several IFD models have incorporated differences in the ability of individuals to compete for resources, with relative and absolute competitive abilities that may vary according to the characteristics of the resource patch (e.g. Sutherland & Parker 1985, 1992, Parker & Sutherland 1986, van der Meer 1997). There is some empirical evidence for such changes in relative competitive ability between resource patches (e.g. Sutherland *et al.* 1988, Grand 1997, Tregenza & Thompson 1998), although in some cases changes in the type of competition occurring between patches could be implicated (e.g. Monaghan & Metcalfe 1985, Inman 1990, Tregenza *et al.* 1996). These individual differences in competitive ability between patches can lead to differential patch preferences within a group of foraging individuals.

Despite the interest in relative competitive ability from both an empirical and theoretical perspective, relatively little is understood about how this measure of ability is affected by different situations. Recent work has examined the effect of patch type (Monaghan & Metcalfe 1985, Inman 1990, Grand 1997, Tregenza & Thompson 1998) and competitor density (Tregenza *et al.* 1996, Humphries *et al.*

1999) on relative competitive ability, but so far the context in which these effects occur has been relatively ignored. The generality of conclusions concerning relative competitive ability has also been questioned as it is almost invariably measured under a specific set of conditions (Tregenza *et al.* 1996, Tregenza & Thompson 1998). Here, using a definition of relative competitive ability as the ability of an individual to compete, under scramble competition, for food items in relation to others within the individual's foraging group, we examine the effect of context on an individual's relative competitive ability.

In order to understand the relative competitive ability of individuals given a free choice between two feeding situations we use variance in food input rate about a set mean as the differentiating factor between two patches. Variance in resource input about a set mean may affect an individual's choice of foraging patch (risk-sensitive foraging theory: Caraco *et al.* 1980, Stephens 1981, McNamara & Houston 1982, Stephens & Charnov 1982, and reviewed in Kacelnik & Bateson 1996). For instance, individuals on a negative energy budget should generally prefer a variable food supply to a fixed one if both have the same mean input rate (Stephens 1981). The relationship between competition and risk-sensitivity has been considered only rarely (e.g. Barnard & Brown 1985) but conclusions from this work indicated that for a given energy requirement, common shrews (*Sorex araneus*) were more likely to be risk-prone when they perceived that they were in competition for resources with another individual.

Using cichlids (*Tilapia zillii*) feeding at continuous-input food patches we examined the relationship between the context in which a feeding patch occurs and the relative competitive ability of the individuals foraging in that patch. We used variance in food input rate about a set mean as the differentiating factor between these two patches and then examined whether relative competitive ability of individuals varied between them. Our approach was to study relative foraging ability in each of two foraging situations in isolation and then to compare our findings with those from the situation where both patches were presented simultaneously.

Methods

Juvenile fish were used in the trials as adult males of this species are territorial (Bruton & Gophen 1992). All fish had been reared in captivity and held for a minimum of six months in glass stock tanks at $23.5 \pm 1^\circ\text{C}$ with a 12L/12D light cycle, conditions that were maintained throughout the experimental period. The 64 fish used in the trials were individually marked under anaesthesia using unique combinations of alcian blue dye marks on the dorsal and anal fins and on the two lobes of the caudal fin. Marking was accomplished by introducing the dye into the fin rays of the anaesthetised fish via a Repette injector system (Jencons (Scientific) Ltd.). Whilst under anaesthetic the fish were also weighed to 0.01 g and measured (standard length, SL, to 0.05 mm). The fish were then randomly divided into eight groups, each of eight fish, which were kept in separate holding tanks for two weeks before the experimental trials began. They were fed *ad libitum* on pelleted trout feed (BOCM Pauls) of the same size as the pellets used in the subsequent feeding trials.

During the experiment each group of fish took part in one two-patch trial then two single-patch trials. Feeding trials were carried out in an arena tank of dimensions $610 \times 307 \times 295$ mm (L \times H \times W) with a water depth of 200 mm. The tank had opaque back and end walls, and a mesh floor raised 15 mm from the base of the tank which ensured that any food items not consumed while falling through the water column were unavailable to the fish during the rest of the trial. In addition, the arena tank contained two submersible water pumps to supply water to the feeders used in the experiment. Vertical marks on the back wall of the tank divided it into three equal-sized sections. An automatic feeder (described in Humphries *et al.* 1999) was mounted at each end of the tank; both were positioned so that the food pellets they delivered fell only into the end sections of the tank. These end sections (defined by marks on the back wall of the tank) are therefore described as the feeding patches and together comprised 66% of the tank length. The arena tank itself was screened off from the rest of the room using black polythene sheeting to avoid visual disturbance. Each two-patch feeding trial consisted of transferring a group of fish to the test arena, allowing them to settle for 30 minutes, then feeding the group a total of 70 pellets (35 from each feeder, which took approximately nine minutes). The pellets, made from ground trout food (BOCM Pauls) mixed with water, were

introduced to the tank by the two computer-driven feeders. The computer controlling the feeders was programmed so that one feeder (left or right, randomised between each trial) introduced 35 pellets at a set interval of one pellet every eight seconds, whilst the other introduced the same number of pellets at intervals randomly generated from a normal distribution with mean of eight seconds and a controlled variance. The distribution of intervals between pellets for this variable feeder was truncated at four and 12 seconds. Thus, the feeders generated two patches with the same mean profitability (7.5 pellets per minute), but with a different variance ($SD \leq 0.01$ for the patch without variance and $SD = 1.77$ for the patch with variance). The two single-patch trials were carried out in a similar way except that only the left-hand feeder was used and 70 pellets were introduced using one input regime ('constant' or 'variable' depending upon the experimental protocol). Trial duration for the single-patch trials was again nine minutes, and the input regimes used were identical to those for the two-patch trial.

After each trial the fish were moved back to their holding tank before being fed to satiation with pelleted trout feed. The trials were carried out on the eight groups on consecutive days and a gap was left between the trials of each group such that all fish had a period of three days without food to standardise hunger and motivation to feed. The two-patch trials were conducted before the single-patch trials to minimise preferences for certain ends of the tank due to memory effects (Milinski 1979, 1984). The experimental trials themselves were arranged in a randomised block design, with half of the trials conducted with the patch with variance on the right, half with it on the left. In addition, the order of the two single-patch trials was arranged such that half of the groups experienced the variable trial first and half experienced the constant trial first (Table 4.1). However, due to the death of a fish partway through the experiment, one of the eight groups (group 8, Table 4.1) was excluded from all analyses.

Table 4.1. Temporal order of the feeding trials. The two-patch trial was experienced first by all groups and the position of the variable patch in this trial was reversed for half of the groups. The order of the single-patch trials was also varied between groups.

| Group | Two-patch trial | First single-patch trial | Second single-patch trial |
|-------|-----------------|--------------------------|---------------------------|
| 1 | Variance right | No variance | Variance |
| 2 | Variance right | No variance | Variance |
| 3 | Variance right | Variance | No variance |
| 4 | Variance right | Variance | No variance |
| 5 | Variance left | No variance | Variance |
| 6 | Variance left | No variance | Variance |
| 7 | Variance left | Variance | No variance |
| 8* | Variance left | Variance | No variance |

* Group 8 was removed from all analyses due to the loss of one individual (see Methods).

All trials were filmed using two VHS video cameras (Panasonic NVMS95 and JVC GR-M7pro), with one camera focused on each patch. The resulting video tapes were analysed in slow motion to allow accurate determination of individual intake rates in each trial, as well as time spent in each patch by all individuals in a group. Single-patch trials, where only one feeder was used, were filmed with a single camera and only individual intake rates were noted. In each trial the fish were ranked according to their food intake, the ranks ran from one to eight, with the fish ranked one obtaining the most pellets in the test. In the two-patch trial this ranking was also calculated separately for intake at each of the two patches. When ties occurred, a mean rank was given to the individuals involved.

All tests for correlation were carried out using the non-parametric Spearman's rank correlation at the group level (i.e. $N =$ eight individuals). For each correlation considered we then tested for heterogeneity among the correlation coefficients of the seven groups (Zar 1996, p384 - 385) before generating a common 'population' correlation coefficient. This common correlation coefficient was then tested using the method of Neyman (in Zar 1996, p384) to check if it was significantly different from zero. Results are presented as mean $r_s \pm SE$, followed by the test statistic and probability value from Neyman's test. All significance values for these tests were corrected using the sequential Bonferroni technique of Rice (1989) and significance at the table-wide level is indicated by an asterisk after the probability value.

Results

In order to check for differences in individual competitive ability under different input regimes we examined the relationship between rank order in the variable single-patch trial and that in the constant single-patch trial. The results indicated a highly significant correlation between the ranks allocated to an individual in the two single-patch trials ($r_s = 0.769 \pm 0.083$, $Z = 5.754$, $P < 0.001$, Fig. 4.1). However, there was a significant difference in the total number of food items eaten by the groups in the two single-patch trials (constant 46.4 ± 16.3 , variable 55.4 ± 9.7 (mean \pm SD); paired t test: $t_6 = 4.32$, $P = 0.005$), with more items being eaten in the variable trial. This shows that the rank order of individual competitive abilities did not change with input regime, despite the intake of the group as a whole being higher in one situation than in the other. Figure 4.2 shows the mean intakes (across seven groups) of fish in both of the single-patch trials, categorised according to their mean rank allocated from the two trials. The similarity of the graphs provides further evidence that the rank order of individual competitive ability did not change with input regime and that there was no change in the relative competitive abilities of individuals between the two single-patch trials.

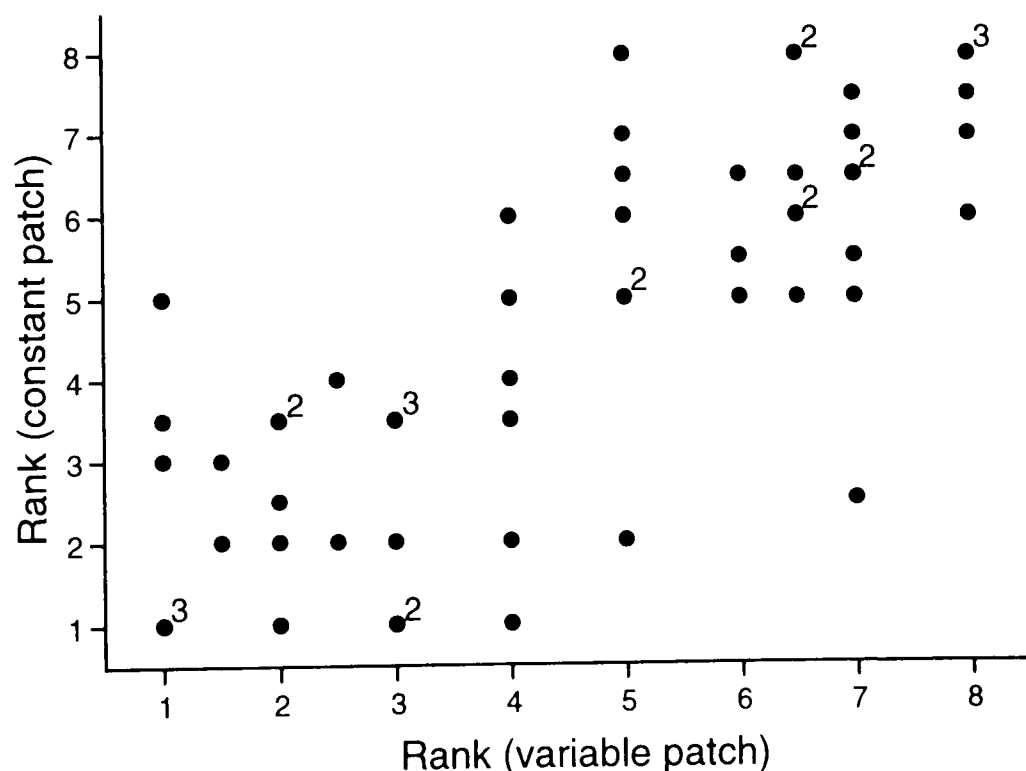


Figure 4.1. Correlation between the rank of competitive ability obtained by the same fish when groups of eight cichlids were fed at a variable and a constant rate in separate trials. Where a point represents more than one individual the number is given next to it.

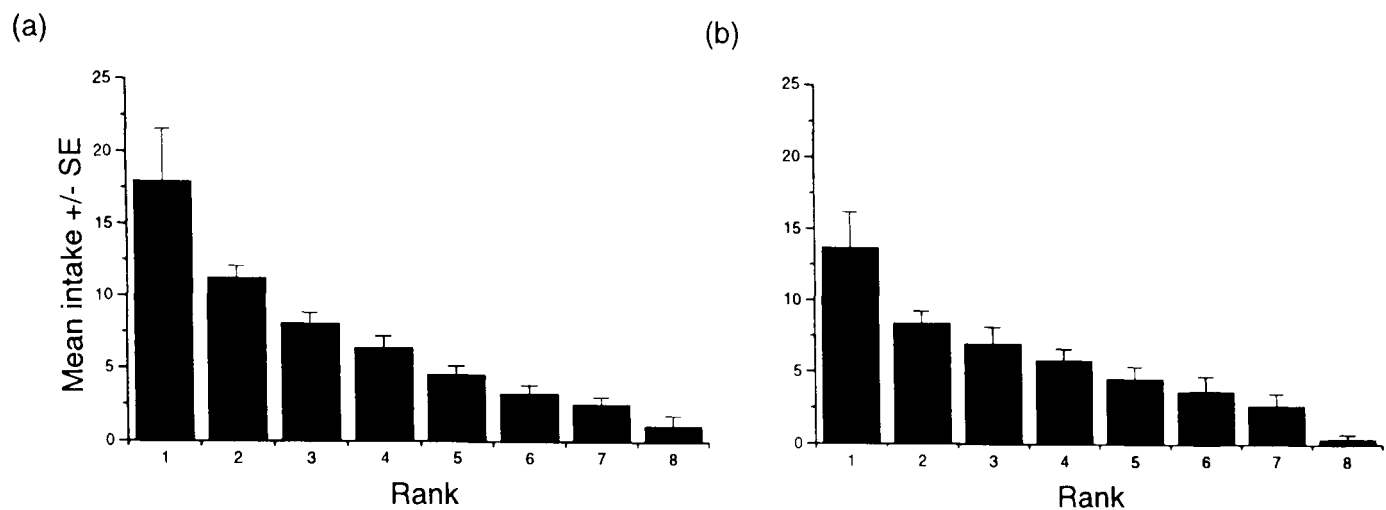


Figure 4.2. The mean intake (across seven groups) of fish of different rank in (a) the variable single-patch trial, and (b) the constant single-patch trial. Bars show mean \pm SE, $N = 7$ fish per rank.

However, when we consider the two-patch trials the relationship between the rank order of individuals and intake is markedly different. We found no correlation between the rank allocated to an individual from its intake in the constant patch and that allocated for the variable patch ($r_s = -0.058 \pm 0.153$, $Z = -0.433$, $P = 0.665$). In addition, we found no relationship between any of the rank orders from the single-patch trials and any of three measures of rank intake from the two-patch trials (Fig. 4.3, Table 4.2). Thus, although a clear ranking existed for both patches in the two-patch trial (Fig. 4.4), an individual's ranking in either of these patches bore no resemblance to its ranking in the other patch, or to its rank from the single-patch trials. In the two-patch trials there was again a significant difference in the total number of food items eaten by a group between the two patches (constant 27.4 ± 2.1 , variable 19.4 ± 6.2 (mean \pm SD); paired t test: $t_6 = -2.60$, $P = 0.040$), but in this instance more items were eaten in the constant patch. We found a significant relationship between the time an individual spent in a patch and its rank for that patch in the two-patch trial (Table 4.3). As expected, individuals that spent more time in a patch tended to obtain more food from it than individuals who spent relatively little time in the same patch.

Table 4.2. Correlations between measures of rank (based on food intake) in single- and two-patch trials.

| | Rank (constant patch, single-patch trial) | Rank (variable patch, single-patch trial) | Rank (summed intake, single-patch trial) |
|--|---|---|---|
| Rank (constant patch, two-patch trial) | $r_s = -0.083 \pm 0.129$, $Z = -0.620$, $P = 0.535$ | $r_s = -0.115 \pm 0.164$, $Z = 0.388$, $P = -0.863$ | $r_s = -0.117 \pm 0.149$, $Z = -0.879$, $P = 0.380$ |
| Rank (variable patch, two-patch trial) | $r_s = 0.139 \pm 0.076$, $Z = 1.039$, $P = 0.299$ | $r_s = 0.256 \pm 0.105$, $Z = 1.919$, $P = 0.055$ | $r_s = 0.248 \pm 0.089$, $Z = 1.854$, $P = 0.064$ |
| Rank (summed intake, two-patch trial) | $r_s = 0.041 \pm 0.142$, $Z = 0.307$, $P = 0.759$ | $r_s = 0.061 \pm 0.194$, $Z = 0.459$, $P = 0.647$ | $r_s = 0.072 \pm 0.172$, $Z = 0.539$, $P = 0.590$ |

Mean r_s values (across seven groups) are shown. No tests approached significance at the table-wide level using a sequential Bonferroni method (Rice 1989).

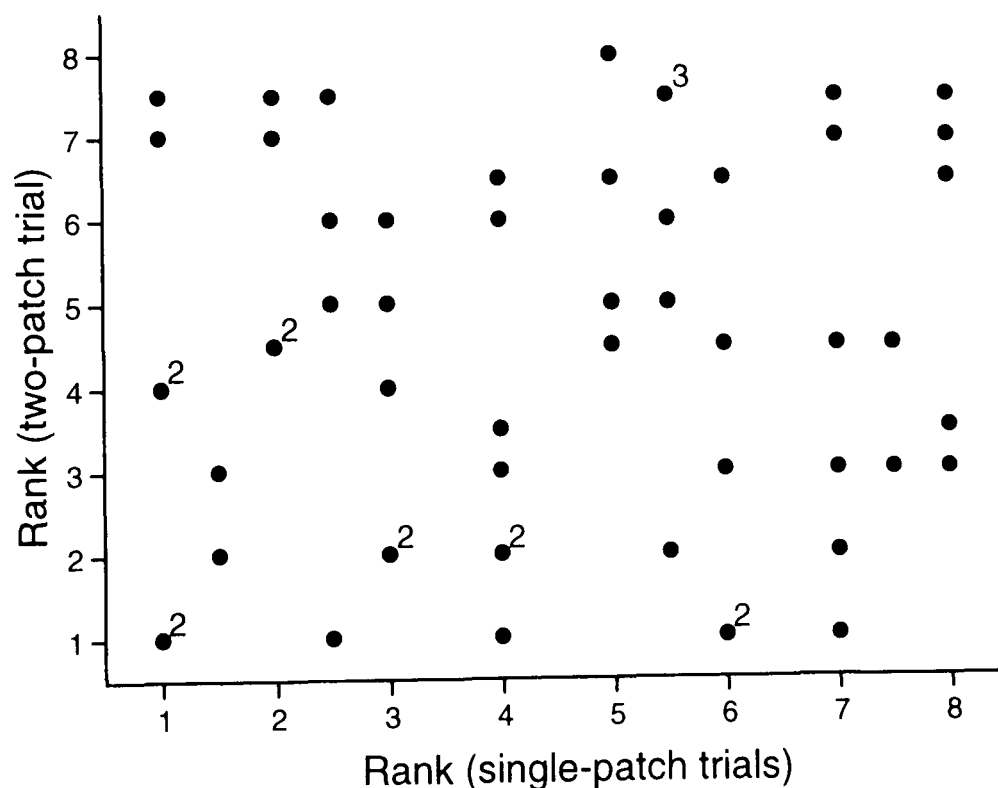


Figure 4.3. Relationship between the overall rank (based on summed intake across trials) from the single-patch trials and that generated when both patches are offered at once (two-patch trials). Where a point represents more than one individual the number is given next to it.

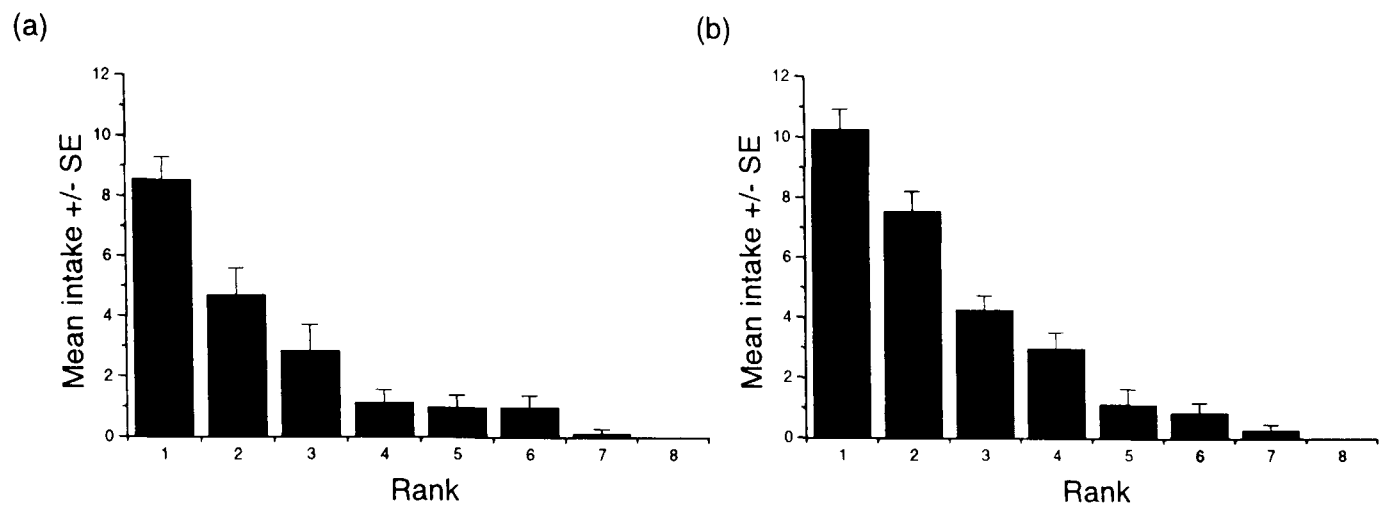


Figure 4.4. The mean intake (across seven groups) of fish of different rank in (a) the variable patch in the two-patch trial, and (b) the constant patch in the two-patch trial. Bars show mean \pm SE, $N = 7$ fish per rank.

Table 4.3. Correlations between measures of rank (based on food intake) and the proportion of time in the two-patch trials spent in either the constant or variable patch.

| | Proportion of two-patch trial spent in constant patch | Proportion of two-patch trial spent in variable patch |
|---|--|--|
| Rank (constant patch, two-patch trial) | $r_s = -0.677 \pm 0.056$, $Z = -5.063$, $P < 0.001^*$ | $r_s = 0.190 \pm 0.214^\dagger$ |
| Rank (variable patch, two-patch trial) | $r_s = 0.356 \pm 0.158$, $Z = 2.666$, $P = 0.008$ | $r_s = -0.633 \pm 0.082$, $Z = -4.734$, $P < 0.001^*$ |
| Rank (summed intake, two-patch trial) | $r_s = -0.226 \pm 0.143$, $Z = -1.693$, $P = 0.090$ | $r_s = -0.267 \pm 0.169$, $Z = -1.998$, $P = 0.046$ |
| Rank (constant patch, single-patch trial) | $r_s = 0.082 \pm 0.163$, $Z = 0.611$, $P = 0.541$ | $r_s = -0.213 \pm 0.124$, $Z = -1.591$, $P = 0.112$ |
| Rank (variable patch, single-patch trial) | $r_s = 0.212 \pm 0.105$, $Z = 1.335$, $P = 0.182$ | $r_s = -0.369 \pm 0.104$, $Z = -2.758$, $P = 0.006$ |
| Rank (summed intake, single-patch trial) | $r_s = 0.163 \pm 0.144$, $Z = 1.221$, $P = 0.222$ | $r_s = -0.333 \pm 0.134$, $Z = -2.489$, $P = 0.013$ |

Mean r_s values (across seven groups) are shown. \dagger indicates significant heterogeneity among the values yielding a mean r_s value. An asterisk indicates significance at the table-wide level using a sequential Bonferroni method (Rice 1989).

When we examined the relationship between rank and size (SL or wet weight) we found no significant correlations (Table 4.4), indicating that there were no size-related differences in relative competitive ability within the groups. In order to look at possible effects of risk-sensitivity on foraging decisions, we classified individuals according to whether they spent a larger proportion of their time in the variable or

the constant patch during the two-patch trial. There was no significant difference in Specific Weight Growth Rate (SWGR) between these two groups (Mann-Whitney U test: $U = 297$, $N_1 = 19$, $N_2 = 37$, $P = 0.346$). Thus, although a few individuals (nine of 56) did have a negative SWGR (indicating a negative energy budget) there was no tendency for these individuals to prefer one patch or the other.

Table 4.4. Correlations between measures of rank (based on food intake) and an individual's size.

| | Rank (summed intake, single-patch trial) | Rank (summed intake, two-patch trial) |
|--------------------|--|--|
| Initial SL | $r_s = 0.025 \pm 0.160$, $Z = 0.187$, $P = 0.825$ | $r_s = 0.258 \pm 0.132$, $Z = 1.932$, $P = 0.053$ |
| Final SL | $r_s = 0.061 \pm 0.158$, $Z = 0.458$, $P = 0.647$ | $r_s = 0.226 \pm 0.146$, $Z = 1.693$, $P = 0.090$ |
| Initial wet weight | $r_s = 0.039 \pm 0.144$, $Z = 0.290$, $P = 0.772$ | $r_s = 0.295 \pm 0.148$, $Z = 2.207$, $P = 0.027$ |
| Final wet weight | $r_s = -0.023 \pm 0.149$, $Z = -0.172$, $P = 0.863$ | $r_s = 0.292 \pm 0.138$, $Z = 2.182$, $P = 0.029$ |

No correlations were judged significant using a sequential Bonferroni method (Rice 1989), applied on a column-wise basis.

Of further interest was whether the fish distributed themselves between the two food patches according to an IFD, and whether the difference in variance between these patches (which is not considered directly by IFD theory) had any effect. Figure 4.5 shows mean numbers of individuals in each patch over time and reveals a relatively stable distribution after an initial settling period. In order to test for an IFD we calculated the mean number of individuals in each patch every 30s to produce seven mean values for each patch. Values were calculated every 30s rather than 10s to reduce the problems of lack of independence between successive data points as the average time (across all individuals) spent in a visit to a patch was 15.6 seconds. The first sampling period was taken to be 60s into the trial in order to exclude the settling period from the analysis. Each of the values represented the mean number of individuals in the patch across all seven trials. There was a significant difference between the numbers of individuals in the two patches, with consistently more fish in the constant patch than in the variable patch (Wilcoxon signed rank test: $Z = -2.37$, $N = 7$, $P = 0.018$). Despite this difference in numbers, we found no difference in the

amount of food eaten per individual at each of the two patches: combined probability test (Sokal & Rohlf 1995, p794) after Wilcoxon signed rank tests on each group of fish, $\chi^2_{14} = 23.69$, $P > 0.05$. Neither did we find that individuals of higher competitive ability were over-represented in the constant patch (the one with more individuals in it), except for the obvious exceptions of ranks generated within that patch (Table 4.3).

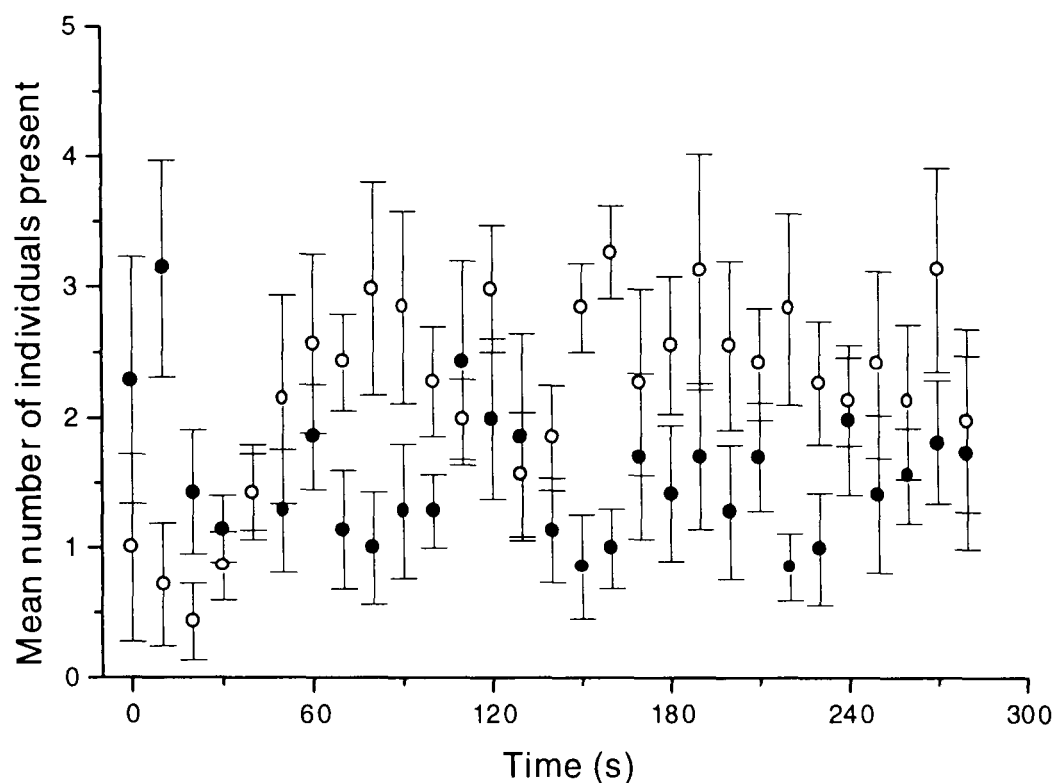


Figure 4.5. Mean number of individuals in each patch of the two-patch trials over time. Filled circles represent individuals in the variable patch, open circles the constant patch. All points are mean \pm SE of seven trials, except those for 270 and 280 seconds, which are means of six and four trials respectively.

The rate at which an individual switched between the two food patches could be considered to give a measure of its sampling rate. We defined a switch between patches as a movement of an individual from one food patch to the other, irrespective of how long it spent in the central area. We found a significant negative correlation between the rate of switching and overall rank (i.e. summed intake of the two patches, Table 4.5). Thus the higher the rate of movement between patches (i.e. sampling rate) the higher the food intake of the fish. However, switching rate in the two-patch trial was not correlated with any of the measures of competitive rank in the single-patch trials (Table 4.5). In addition, there was a correlation between rank and the number of forays from the central section to one of the food patches ($r_s = -$

0.477±0.103, $Z = -3.570$, $P < 0.001$). The number of forays was calculated as number of visits to either food patch minus the number of switches that the individual performed. These results indicate that better competitors spend the most time in, or make the most visits to, food patches. We were unable to differentiate between these two possible explanations by testing for correlation between rank and overall time spent in a food patch (as opposed to in the central section) because tests indicated that the seven r_s values were not drawn from the same population ($\chi^2_6 = 16.038$, $P = 0.014$). However, when the outlying correlation coefficient (group 3, $r_s = -0.964$) was removed and the tests conducted on the remaining six values, a significant negative correlation between rank and time spent outside the central section was found ($r_s = -0.381 \pm 0.165$, $Z = -2.637$, $P = 0.008$). The fact that the correlation coefficient that was removed also indicated a very strong negative correlation leads us to suggest that an overall negative correlation is a valid one, and thus that poor competitors tended to spend more time in the central section whilst the better competitors fed.

Table 4.5. Correlations between measures of rank (based on food intake) and the switching rate between food patches in the two-patch trial.

| | Correlation coefficient |
|---|---|
| Rank (constant patch, single-patch trial) | $r_s = -0.127 \pm 0.179$, $Z = -0.950$, $P = 0.342$ |
| Rank (variable patch, single-patch trial) | $r_s = -0.196 \pm 0.214$ † |
| Rank (summed intake, single-patch trial) | $r_s = -0.150 \pm 0.187$, $Z = -1.121$, $P = 0.262$ |
| Rank (constant patch, two-patch trial) | $r_s = -0.286 \pm 0.121$, $Z = -2.141$, $P = 0.032$ |
| Rank (variable patch, two-patch trial) | $r_s = -0.425 \pm 0.117$, $Z = -3.184$, $P = 0.001$ * |
| Rank (summed intake, two-patch trial) | $r_s = -0.427 \pm 0.141$, $Z = -3.192$, $P = 0.001$ * |

Mean r_s values (across seven groups) are shown. † indicates significant heterogeneity among the values yielding a mean r_s value. An asterisk indicates significance at the table-wide level using a sequential Bonferroni method (Rice 1989).

Discussion

Our results show that in trials where only one input source is available, relative competitive ability is preserved whether the input rate is constant or variable. The rank order of an individual does not appear to change with input regime, nor does its competitive ability relative to others in the group. In contrast, when the groups were given a choice between the two types of patch within the same trial, the rank

ordering of individuals on intake was correlated neither between patches, nor with the ordering generated from the single-patch trials. Increased temporal clumping of resources leading to a decrease in monopolisation of the food source by dominant individuals (Grant & Kramer 1992) is unlikely to be applicable to our results. Although temporal clumping occurred in the variable patch, it was limited to a maximum such that only single items were available at any instant, and had an upper limit. In addition, the random nature of the input with variance made it inherently unpredictable, and thus dominants may not have risked chasing off a subordinate when there was a chance of another item arriving at any time. Further, if reduced monopolisation of resources were occurring, we would expect the intakes in the variable patch to be less skewed than in the patch with a constant input rate, which was not the case. The difference in intakes between the two best ranks, although relatively large, does not suggest to us that the best individuals were able to effectively monopolise the patch in either case, nor did we see any evidence of fish being intimidated from taking pellets in either of our trial types.

The lack of correlation between an individual's rank in the two types of trial (single- and two-patch) could be attributed to a number of factors. The most obvious is the effect of reduced competitor density at the two patches compared with a single-patch trial. The single-patch trial results indicate the relative competitive abilities for a group of eight fish, and this will only be a good guide if relative competitive ability is constant across different competitor densities. Recent work suggests that in both continuous input situations and systems where less extreme interference competition occurs, relative competitive ability is not constant irrespective of group size (Tregenza *et al.* 1996, Cresswell 1998) and, more specifically, changes differentially with relative rank of the individuals being examined (Humphries *et al.* 1999). However, further work does suggest that the rank order of the individuals involved is less likely to change than the relative differences between the ranks (Humphries *et al.* 1999, S Humphries, G D Ruxton & N B Metcalfe unpublished data).

When we consider the results concerning switches between patches and forays from the central section another explanation reveals itself. In single-patch trials, individuals that are able to competitively exclude others or that have a faster speed of

reaction to a falling pellet over short distances within a patch are likely to gain an advantage over others in terms of food acquisition. However, in the two-patch trial, the added qualities of speed of movement over longer distances between patches and the ability to monitor the other patch would appear to be equally (if not more) important. It is clear from the lack of correlation between rankings in different trials that individuals with traits that are advantageous in one situation do not necessarily have the traits that are important in the other. Therefore, if some individuals differ in abilities with respect to traits such as these then it is likely that some will be better able to acquire food in one situation than the other, leading to differences in intake (and hence rank) between the two types of trial.

Because all of the two-patch trials were completed before the single-patch ones, it is possible that the effects that we interpret as being due to the differences between one and two patches can be explained by changes in fish behaviour over time. However, whilst we cannot eliminate this possibility, we would argue that the two week settling period in which the individuals were kept in their experimental groups before the start of the experiments makes such an explanation based on a learning effect during the trials unlikely.

A situation where patches may have the same mean input but differ in variance is an untested one in IFD theory. Milinski (1984) reports an experiment where both patches had variance but had different mean input rates, but this addresses the question of perception of differences in mean gain, not variance when gains are equal. Milinski's distributions became stable during the trial, with very little switching between patches. Our measure of switching rate suggests that individuals that were able to obtain more food in the two-patch trials ('good' competitors) were also the ones who were sampling their environment the most, although, as with Milinski's fish, our mean sampling rates were relatively low with 2.89 ± 2.13 switches per individual per trial (mean \pm SD). However, our results are in contrast to the findings of Milinski (1984) and the predictions of Regelman (1984) that better competitors distribute themselves in the ratio of patch profitabilities before poor competitors and that poor competitors do so after switching more often between the patches than better competitors. This could imply that, in our experiment, individuals

that sampled the environment more were better able to track feeding opportunities, and that these individuals were thus generally judged better competitors in the two-patch trial (Table 4.5). However, we would suggest that if better competitors switch more (rather than more switching leading to the individual increasing its intake), and because of the overall low rate of switching, our results indicate a cost to switching between patches which could decrease the fit to an IFD, even in the relatively small confines of the experimental tank. Our plot of number of individuals in each patch at set intervals appears similar to ones from previous work by Milinski (1979, 1984) on three-spine sticklebacks (*Gasterosteus aculeatus*), in that there is an initial settling period, followed by a relatively flat distribution. However, whilst Milinski found a fit between the distributions of his fish and those predicted by IFD theory, our distributions do not match the predictions for a two patch model with equal input rates. The concept of risk-sensitive behaviour may help explain this deviation from an IFD. The significant difference between the numbers of individuals in the two patches, with consistently more fish in the constant patch than in the variable patch, suggests that the fish in this experiment may have been risk-averse. Risk-proneness is the usual state of animals subjected to variation in the delay between resource items (Kacelnik & Bateson 1996), but the effect is likely to be reduced or reversed if the animals are on a positive energy budget. Barnard and Brown (1985) found that shrews became more risk-prone in the presence of competitors due to the expected effects of competition (the perception that the patch would become depleted more quickly). In the case of our continuous-input patches where depletion is at its most extreme, the effects of competition may well influence an individual's tendency towards risk-proneness or aversion. The absence of a preference for one or other patch by individuals with a negative energy budget indicates that if risk-proneness is operating in these individuals it is likely to be outweighed by other factors. The use of continuous-input food sources in our trials meant that they met the criterion that competition increased the probability of finding nothing at the potential feeding sites, and thus risk-aversion may have occurred because the probability of finding nothing at the low variance site is lower than at a high variance site (Barnard & Brown 1985). Thus, a combination of a positive energy budget for the majority of individuals and the effect of a continuous-input regime may explain the distribution that we found.

In summary, our results strongly suggest that an individual's relative competitive ability is dependent upon the context of the foraging situation. Both models and empirical work support the idea that relative competitive ability may change between patches. However, we suggest that in some cases this will be dependent upon the context in which the resource patches are encountered. We found a strong correlation between rankings of individuals in the two situations in isolation. Given this result it would be reasonable to expect that this ranking would also carry over to the more complicated situation where individuals have a free choice between the two feeding situations. However, although we find that there is a clear ranking of individuals in the two-patch situation, this ranking is markedly different from that obtained in the two separate situations. We suggest that individuals that do well in the single-patch trials may not be as successful in obtaining food in the two-patch trials as this situation rewards individuals with different and/or additional attributes. It is clear from the lack of correlation between rankings in different trials that individuals with traits advantageous in one situation do not necessarily have the traits that confer a similar advantage in the other one. Indeed, we would suggest that relative competitive ability in different situations might depend less on an overall measure of ability or quality than on morphological or behavioural trade-offs.

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**UNEQUAL COMPETITOR IDEAL FREE DISTRIBUTIONS: PREDICTIONS
FOR DIFFERENTIAL EFFECTS OF INTERFERENCE BETWEEN PATCHES**

Abstract

Unequal competitor ideal free distribution (IFD) models that deal with the effects of interference allow for the relaxation of several unrealistic assumptions of the basic IFD model. Here we use a recently proposed interaction-matrix method to examine the general case where the effect of interference can vary between patches, one previously unexplored in the literature. Simulations from an individual-based model reveal a decrease in the number of stable equilibrium distributions as the competitive advantage of the dominant phenotype declines in one patch. This leads to a case where a single stable equilibrium is produced, in which both phenotypes are found on both patches. Furthermore, this single equilibrium manifests itself at a point when the advantage of the better phenotype is still relatively large. Such a dynamic pattern of distributions is not predicted by classical interference IFD theory and may help explain the lack of certain predicted distributions in empirical tests of the theory.

Introduction

The ideal free distribution (Fretwell & Lucas 1970, Fretwell 1972) is an important pillar of theoretical ecology and forms the basis of most attempts to predict the distribution of individuals between different resources. In the ideal free distribution (IFD) as originally defined, individual animals are equal in their competitive abilities, are free to move between resource patches, and have perfect knowledge of the qualities of all available patches. These assumptions lead to perfect matching between the quality of a resource patch and the number of animals that use it. At this distribution, no individual can improve its rate of resource acquisition by moving to another patch. Much attention has been given to elaborating the model to include more realistic assumptions (see Tregenza 1995 for an overview) and the IFD has been extensively tested, modified and improved. In particular, many studies have relaxed the assumption that all individuals are intrinsically equal in their competitive ability. However, these studies, almost without exception, assume that the ratio of the competitive abilities of two phenotypes will remain unchanged, regardless of the identity of the patch that they occupy. For instance, if phenotype A has twice the competitive ability of phenotype B in one patch of the system, then it is assumed that it will have twice the competitive ability of B in all patches in that system, even if the absolute competitive abilities of the two phenotypes change between patches. This assumption has not been verified empirically, indeed, there is growing evidence that it does not hold in some systems (Tregenza & Thompson 1998, Humphries *et al.* in press, and Cresswell W, Smith RD & Ruxton GD, unpublished data). Hence, the purpose of this paper is to explore the consequences of relaxing the assumption of patch-independent relative competitive ability in IFD models.

For comparative purposes, we first briefly summarise the predictions of published IFD models where relative competitive abilities of different phenotypes are assumed to be patch-independent. Historically, IFD models have been split into two types according to resource availability: “continuous input systems” where resources are fed into a patch at a fixed rate and are consumed immediately; and “interference models” where there is a standing crop of resources and individuals experience a short-term, reversible decline in acquisition rate due to the presence of others in the patch (Goss-Custard 1980, Sutherland 1983). We will confine our attention to the

second of these classes, although some brief discussion of previous work on the other class will also be required. The most studied case is that where individuals belong to two different phenotypes and have a choice between two different resource patches. The most influential unequal-competitor models dealing with this situation are those of Sutherland and Parker (Sutherland & Parker 1985, 1992, Parker & Sutherland 1986). For the two phenotype, two patch case with interference their models predicts only one Evolutionarily Stable Strategy (ESS) distribution, the 'truncated phenotype' distribution. That is, a distribution where at least one of the phenotypes is confined to only one of the patches. In contrast, recent work by van der Meer (1997) makes the assumption that the relative competitive ability of an individual in a patch should be judged against the sum of all the individuals in the patch (rather than the average of those individuals, as used by Sutherland and Parker). This apparently small change leads to radically different predictions from those of Sutherland and Parker. Van der Meer's models predict that for a given set of circumstances many different ESS solutions will be stable (the one to which a system eventually settles being determined by initial conditions). Furthermore, almost all of these solutions are of a mixed type, where both phenotypes occur on both patches.

For continuous input systems, Sutherland and Parker's "comparison to the mean" assumption leads to multiple ESSs in the classical case where the relative competitive ability of individuals do not differ between patches (Sutherland & Parker 1985, 1992, Parker & Sutherland 1986, Houston & McNamara 1988). Parker and Sutherland (1986, Sutherland & Parker 1992) explored the effects of adding between-patch differences in relative competitive ability to this model structure. This modification had a dramatic effect on model predictions, specifically it results in the emergence of a single ESS which is always of the truncated phenotype form. Hence, at least for the continuous input situation, it is clear that predictions of simple models where the ratio of competitive abilities does not change between patches are structurally unstable, and slight deviations away from this assumption of constant relative competitive abilities lead to radically different model predictions. In this paper we explore the consequences of relaxing this assumption for the alternative interference-based situation. Specifically, we use the interaction-matrix method of

van der Meer (1997) and thus investigate the consequences of having different interaction matrices for the two patches.

The model

We consider a simple environment with two patches, denoted p and q , and wish to find ideal free distributions of unequal competitors in this environment. Each competitor belongs to one of two different phenotypes, A or B , the numbers of individuals belonging to each phenotype being N_A and N_B . Interference between individuals is described by the interference matrix approach of van der Meer (1997). Specifically, we assume that the interference a focal competitor experiences is the sum of the effects of every individual in the patch. The effect of one individual on another is described by the quotient of their competitive abilities. We denote the competitive abilities of the two phenotypes on patch p as K_{Ap} and K_{Bp} . Similarly, they are K_{Aq} and K_{Bq} on patch q . We further denote the number of A individuals on patch p as A_p , with A_q , B_p and B_q being likewise defined.

The resource acquisition rate for an A individual on patch p is given by

$$E_{Ap} = R_p \left(A_p \left(\frac{K_{Ap}}{K_{Ap}} \right) + B_p \left(\frac{K_{Bp}}{K_{Ap}} \right) \right)^{-m} \quad (1)$$

where R_p is a simple constant, describing the intrinsic quality of the patch, and m is the interference constant (Hassell & Varley 1969, Sutherland 1983).

Similarly, the resource acquisition rate of a B individual on patch p is given by

$$E_{Bp} = R_p \left(A_p \left(\frac{K_{Ap}}{K_{Bp}} \right) + B_p \left(\frac{K_{Bp}}{K_{Bp}} \right) \right)^{-m} \quad (2)$$

Each simulation presented here consists of 72 individuals, 36 of each of the two phenotypes, and starts with every individual randomly and independently assigned to one of the two patches (each with probability 0.5). However, additional simulations

(not presented here) have shown that none of our results are sensitive to this assumption. Individuals are then selected at random and if the selected individual could increase its resource acquisition rate by moving to the other patch then we switch that individual across. This is repeated until no individual would benefit by moving, i.e. when an equilibrium distribution has been achieved.

Model predictions

We first consider the condition where relative competitive ability is constant between patches, i.e.

$$\frac{K_{Ap}}{K_{Bp}} = \frac{K_{Aq}}{K_{Bq}} \quad (3)$$

This is the situation considered by van der Meer (1997). In agreement with his results, our simulations show no occurrence of truncated phenotype distributions, but rather that one set of parameter values can lead to numerous different (but generally always mixed) stable ESS's. For example, figure 5.1 summarises the outcome of 1000 simulations of the type described above. Each trial was run using the same parameter values, but differed due to the stochasticity in the algorithm used to distribute individuals between patches at the start of the simulation and that used to select individuals for movement. We plot frequency of occurrence of both phenotype *A* (dark shade) and phenotype *B* (light shade) occurring in patch *p* when equilibrium is reached. In all cases the simulation resulted in a stable equilibrium. However, for this given set of conditions, there was considerable variation in the form and frequency of occurrence of these equilibria. In total, we find that for this set of parameter values, eight different mixed equilibria are possible. The relative likelihood of these equilibria differs; for example, we found that the equilibrium where 33 individuals of phenotype *A* and 21 individuals of phenotype *B* occurred in patch *p* occurred in only one of the 1000 simulations shown, whereas the equilibrium where patch *p* contained 29 individuals of phenotype *A* and 29 individuals of phenotype *B* occurred more than 300 times. This observation of numerous alternative mixed ESS's was found for a very wide range of parameter combinations, except for

the case where interference was so low that all individuals exploited the better patch (figure 5.2).

We now examine the novel case where the relative competitive abilities of the two phenotypes differ between patches, i.e.

$$\frac{K_{Ap}}{K_{Bp}} \neq \frac{K_{Aq}}{K_{Bq}} \quad (4)$$

In patch q phenotype A is still better than phenotype B by a factor of two, however, in patch p we now reduce the advantage to a factor of 1.85. Examination of figure 5.3b shows that the effect of this modification on model predictions is very dramatic: there is now only one ESS, and this is mixed. Importantly, this result is robust for a wide range of parameter values (simulations not shown). This reduction in the number of possible ESS distributions mirrors Sutherland and Parker's work on continuous input systems where they predicted that breaking the assumption of spatial homogeneity of relative competitive ability would lead only to situations where there is a single ESS (Parker & Sutherland 1986, Sutherland & Parker 1992). However, there are important differences between our results and theirs. Firstly, they predict that only truncated phenotype distributions are possible, whereas the distribution that we find above is mixed. Furthermore, if we decrease the difference between the two patches in their effect on relative competitive ability then we recover the situation where there are multiple ESS's, most of which are mixed (figure 5.3c). This change in the number of possible distributions is, unlike the dramatic discontinuity found in Sutherland and Parker's model, a continuum from a single ESS through to multiple stable distributions.

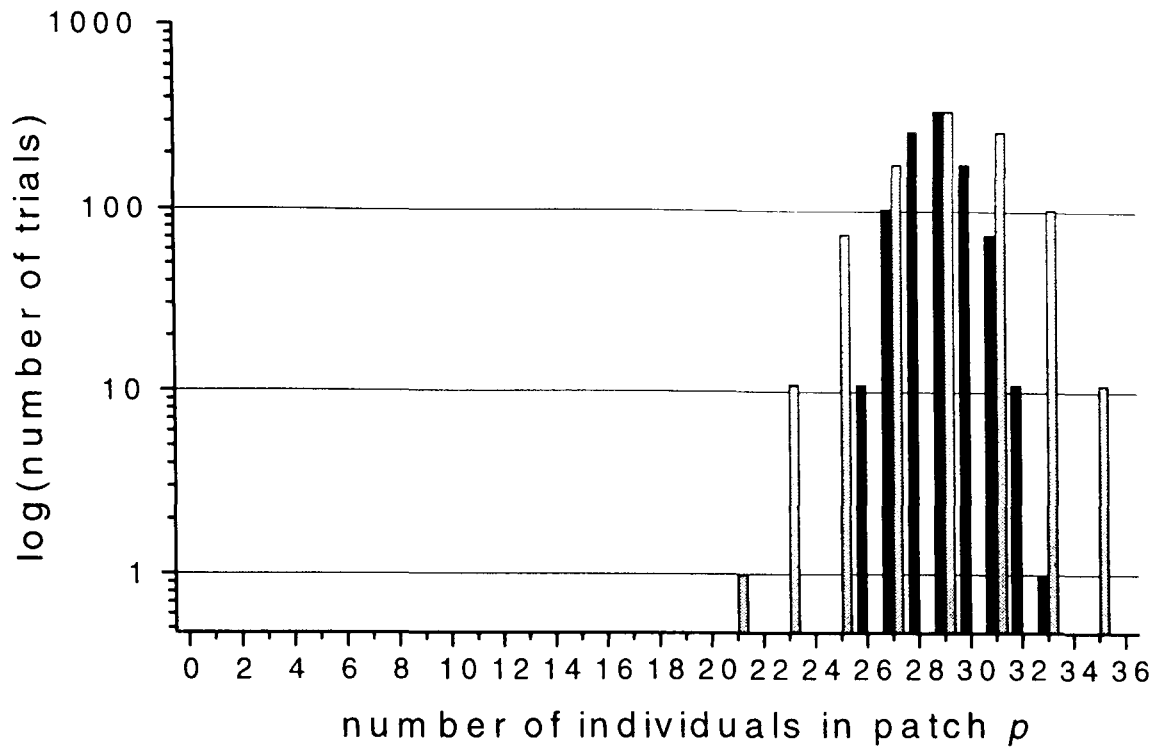


Figure 5.1. Histogram summarising the results of 1000 simulations of the two phenotype model using the following parameter values: $m = 0.5$, $N_A = N_B = 36$, $K_{Ap}:K_{Bp} = K_{Aq}:K_{Bq} = 2:1$, $R_p:R_q = 2:1$. The bars describe the frequency with which various numbers of phenotype A (dark shade) and phenotype B (light shade) occurred on patch p (the higher quality patch) at the final equilibria. Since there are eight bars of each shade this tells us that eight different equilibria are possible as for each frequency of phenotype A there can only be one frequency of phenotype B. For example, we see that an equilibrium where 33 A individuals and 21 B individuals finished on patch p (and consequently 3 A and 15 B on patch q) occurred only once in these simulations.

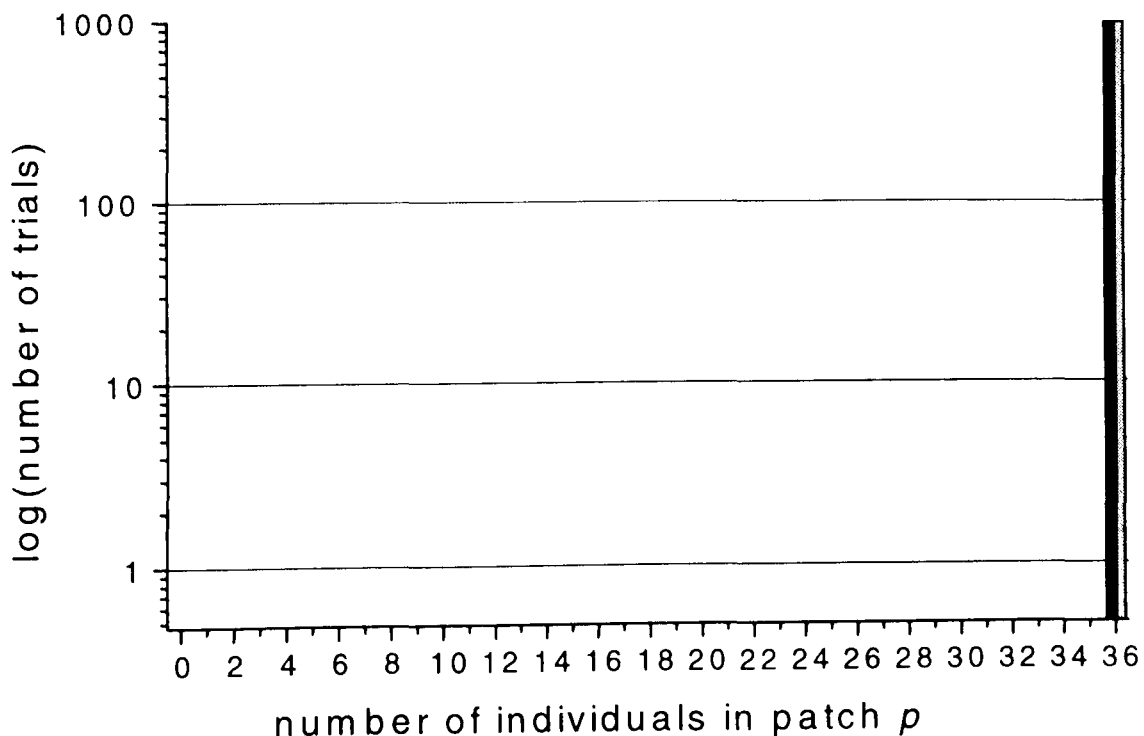


Figure 5.2. As figure 5.1, but with $m = 0.1$. We now find that all simulations result in an equilibrium where all individuals congregate in patch p , the more profitable patch, due to the low value of m and hence the negligible effect of competitor density on resource acquisition rate.

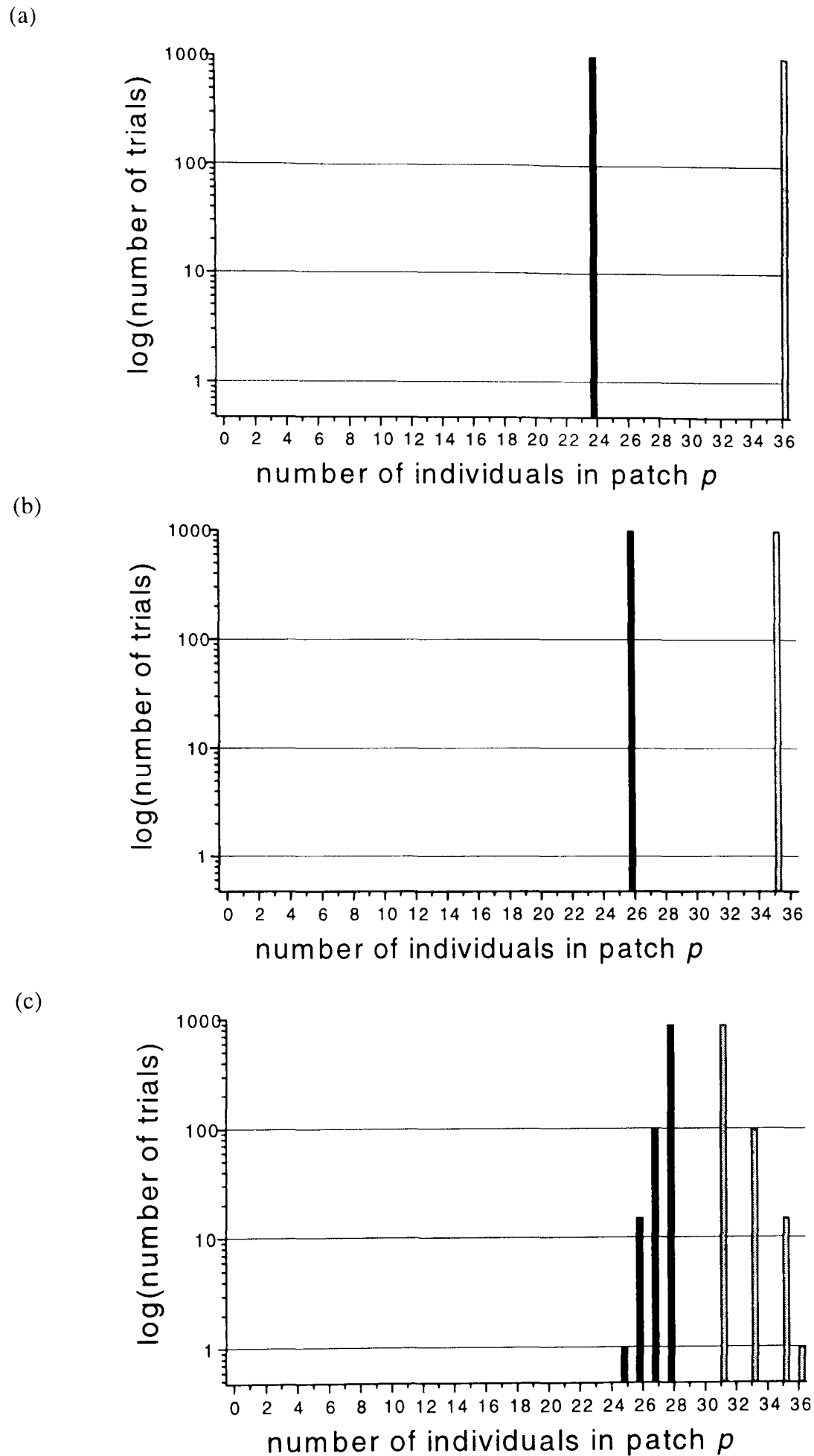


Figure 5.3. As figure 5.1, but with (a) $K_{A_p}:K_{B_p} = 1.5:1$, (b) $K_{A_p}:K_{B_p} = 1.85:1$ and (c) $K_{A_p}:K_{B_p} = 1.86:1$, while $K_{A_q}:K_{B_q} = 2:1$ for all cases. Only a single mixed equilibrium is found where both phenotypes are found on each patch, until the ratio of abilities reaches 1.85, where a transition occurs from the single mixed distribution to a number of stable solutions, most of which are mixed.

Discussion

Our use of van der Meer's (1997) interaction-matrix method for the case where the ratio of the two phenotype's relative competitive abilities do not differ between patches confirms the observation that truncated phenotype distributions are not always predicted when competitors differ in relative competitive ability (Sutherland & Parker 1985, 1992, Parker & Sutherland 1986). Additionally, when differences in both prey searching and prey handling efficiencies are examined separately, differences in the types of distribution produced are predicted. Holmgren (1995) has shown that phenotypic differences in the prey searching efficiency lead to a truncated phenotype distribution, whilst differences in prey handling efficiency produce a distribution that is partially segregated. Thus, it is now clear that truncated phenotype distributions are not necessarily predicted for all unequal competitor IFDs.

There is very little evidence to suggest that true truncated phenotype distributions actually occur in the field or lab, and various reasons why imperfect truncation (partial truncation) might occur have been discussed (Parker & Sutherland 1986, Milinski & Parker 1991). Correlational evidence does exist for such partially truncated distributions and comes from work on herring gulls (*Larus argentatus*: Monaghan 1980, Monaghan *et al.* 1986), oystercatchers (*Haematopus ostralegus*: Goss-Custard *et al.* 1984), black grouse (*Tetrao tetrex*: Alatalo *et al.* 1992), mute swans (*Cygnus olor*: Milinski *et al.* 1995) and common cranes (*Grus grus*: Bautista *et al.* 1995). We suggest that the lack of true truncated phenotype distributions found in these empirical tests of unequal competitor IFDs may be due to violations of the assumption of constant relative competitive ability, and that it may not therefore be necessary to invoke many of the arguments previously put forward for the lack of true truncation in empirical tests.

When phenotypic differences in relative competitive ability between patches are considered for the interference case, our model produces a range of distributions, the number of which decreases as the ratio of competitive abilities on the poor patch tends to one. This continuum of distributions is a result of relaxing the assumption of very large population sizes made in most analytical treatments of IFD theory. Such a

dynamic pattern of distributions is not predicted by classical interference-IFD models for any situation of which we are aware. This variation in the number of stable distributions with changes in the ratio of relative competitive abilities between patches clearly invites empirical examination. In general, we find that the match between our results for an interference system and those of Sutherland and Parker for a continuous input system is best when the number of individuals is large and the difference between the two phenotypes is also sufficiently large. The first of these is to be expected since infinitely large population sizes are an implicit assumption of their analytic approach.

The assumption of constant relative competitive ability appears to have been seldom questioned, and then only for the continuous input situation (Sutherland & Parker 1985, 1992, Parker & Sutherland 1986). In this case, phenotypic differences in relative competitive ability between patches only ever produce one ESS distribution, which is always a truncated phenotype distribution. Although the relative payoffs of individuals of different ability change across patches in interference IFD models, this differs from the above continuous input case because the effect of interference is density dependent, and thus the differences are not intrinsic to the patches themselves. These patch-specific differences generate the novel predictions that we present here.

We use the interaction-matrix method developed by van der Meer (1997) for a number of reasons. Firstly, it enables relatively complex concepts, such as the between-patch differences in relative competitive ability modelled here, to be integrated into IFD models by use of different matrices for different situations. We feel that the flexibility of this method in describing interactions between individuals has great potential for further developments of IFD theory in the future, and may well lead to a greater understanding of the many different ways in which competition can occur. In addition, we believe that the interaction-matrix method provides a biologically more realistic description of interference competition in that an individual's reward is a function of the sum of the amount of interference that it experiences from each of its competitors. Recently it has been argued that, using the Sutherland-Parker model of interference, in certain cases individuals may actually

obtain increasing rewards with increasing numbers of conspecifics (van der Meer 1997, Weber 1998). However, the lack of biological realism suggested by van der Meer (1997) has been questioned (Sutherland & Parker 1998, Ruxton 1999) and it is probable that the Sutherland-Parker model still provides a good description of some competitive situations.

The novel integration of phenotypic differences in relative competitive ability between patches into an interference IFD model, and the subsequent differences on the effect of interference on a given phenotype, clearly has important implications for the distributions of individuals between those patches. The use of van der Meer's (1997) interaction-matrix method to describe the effects of interference on resource acquisition rate provides us with a new tool with which to investigate interference in social groups. Incorporated into our individual-based model it provides a number of original predictions for unequal-competitor interference IFDs that may help explain the lack of true truncated-phenotype distributions in the empirical literature.

Acknowledgements

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**NON-COMPETITIVE PHENOTYPIC DIFFERENCES AND THE IDEAL FREE
DISTRIBUTION**

Abstract

1. We present a model of the ideal free distribution (IFD) where differences between phenotypes other than those involved in direct competition for resources are considered. We show that these post-acquisitional differences can have a dramatic impact on the predicted distributions of individuals.
2. Specifically, we predict that, when the relative abilities of phenotypes are independent of location, there will be a continuum of mixed ESS distributions (where all phenotypes are present in all patches).
3. When differences in the post-acquisitional trait are considered to differ between patches, however, we predict only a single Evolutionarily Stable Strategy (ESS) at equilibrium. Further, this distribution may be fully or partially segregated (with the distribution of at least one phenotype being spatially restricted), but it will never be mixed.
4. Our results for post-acquisitional traits therefore mirror those of Parker (1982) for direct competitive traits. This comparison illustrates that irrespective of whether individual differences are expressed before or after competition for resources, they will still exert considerable influence on the distribution of the individuals concerned.

Introduction

To date, all variants of classical ideal free distribution theory (Fretwell & Lucas 1970; Fretwell 1972) have considered resource acquisition rate as the fitness correlate for Fretwell and Lucas' 'suitability' of a patch. Resource acquisition (gain) is usually determined by a measure of an individual's relative competitive ability within the population, and this has been shown to vary between individuals in many taxa (e.g. fish: Milinski 1982, birds: Harper 1982, and fishermen: Gillis *et al.* 1993). However, these competitive differences are by no means the only differences that one finds between individuals.

A source of inter- and intraspecific variation that is commonly considered by physiological ecologists is that arising from differences in the efficiency with which animals process the food that they obtain. Such post-acquisitional differences may include (but are not limited to) digestive efficiency, metabolic efficiency, and growth. Documented variation in these traits includes differences in metabolic efficiency between size classes of fish (e.g. Brett & Groves 1979, Wootton 1994), differing digestive efficiencies between birds (e.g. Afik & Karasov 1995), and between-individual differences in growth efficiency in fish (Carter *et al.* 1993a, b, McCarthy *et al.* 1993, 1994). These differences may be related to one or more of an individual's gender, size, age, reproductive status or 'quality'. Similarly, interspecific differences can exist in many of the same traits. For instance, marked variation in digestion parameters has been noted between related species feeding on the same diet in both seabirds (Jackson 1992, Hilton *et al.* in press) and birds of prey (Barton & Houston 1993a, b).

Even if the differences between individuals or species in such post-acquisitional traits are not as large as those commonly considered for competitive ability, they can still have dramatic effects on the individuals concerned. For instance, variation in the protein degradation rate between individual rainbow trout *Oncorhynchus mykiss*, leads to some individuals growing faster for the same ration than others, due to their increased efficiency in converting protein in their food into new tissue (McCarthy *et al.* 1994). The increased growth rates of the more efficient individuals can thus have far reaching effects on their subsequent growth (McCarthy *et al.* 1994). Thus,

although an individual may be able to effectively gather resources from its environment, the way in which it deals with these resources afterwards is equally important. It is therefore likely that post-acquisitional differences will have an effect on the distribution of animals by their effect on such factors as the efficiency of use of the resources gained or how those resources are allocated by the individual to different processes.

Here we examine the effects of introducing post-acquisitional phenotypic differences into a continuous input IFD model similar to that of Parker (1982). We use an analytical approach to determine how animals differing in non-competitive traits should partition themselves between resource patches. The importance of intra- and inter-species differences in traits other than those directly involved with competition for resources suggests that their effect on animal distributions could have far-reaching consequences for such diverse areas as niche partitioning, social foraging and species divergence.

Model definition

The model considers two phenotypes (A and B), with total population sizes P_A and P_B . There are two patches (i and j), which have resource input rates Q_i and Q_j .

Phenotypes A and B are equally effective at sequestering resources. However, they have different abilities to convert these resources into useable energy. Further, the conversion efficiency of each phenotype differs between the two patches. K_{Ai} is the conversion efficiency (i.e. fraction of acquired resource that is converted to useable energy) of phenotype A on patch i . We also have K_{Aj} , K_{Bi} and K_{Bj} . The fraction of individuals of phenotype A that are in patch i is defined as p_{Ai} . Similarly, we have p_{Aj} , p_{Bi} and p_{Bj} . These fractions are by definition, related thus:

$$p_{Aj} = 1 - p_{Ai} \tag{1}$$

$$p_{Bj} = 1 - p_{Bj} \tag{2}$$

The resources available in a patch are divided equally between all the occupants of that site, and so the rate of energetic gain of an individual of phenotype B in patch j is

$$\frac{K_{Bj}Q_j}{C_j} \quad (3)$$

where C_j is the total number of individuals on patch j :

$$C_j = p_{Aj}P_A + p_{Bj}P_B. \quad (4)$$

Naturally, the same reasoning extends to any individual on either of the two patches.

Evolutionary stable distributions

Any distribution of individuals between patches is uniquely described by the pair $\{p_{Ai}, p_{Bj}\}$. We wish to find ESS values on this pair, i.e. pairs of values such that individuals of neither phenotype would increase their fitness (in this case based on maximisation of energetic gain rate) by moving to the other patch.

We begin by looking for mixed ESS distributions, that is, ESS distributions where both phenotypes are present on both patches. i.e. where the ESS pair satisfies

$$0 < p_{Ai}; p_{Bi} < 1. \quad (5)$$

We require that the energetic payoff to each phenotype is the same in both patches. Therefore, we must simultaneously satisfy the following

$$\frac{Q_i K_{Ai}}{C_i} = \frac{Q_j K_{Aj}}{C_j} \quad (6)$$

and

$$\frac{Q_i K_{Bi}}{C_i} = \frac{Q_j K_{Bj}}{C_j} \quad (7)$$

This requires that

$$\frac{Q_i K_{Ai}}{Q_j K_{Aj}} = \frac{Q_i K_{Bi}}{Q_j K_{Bj}} = \frac{C_i}{C_j}, \quad (8)$$

which implies that

$$\frac{K_{Ai}}{K_{Aj}} = \frac{K_{Bi}}{K_{Bj}} = \frac{Q_j C_i}{Q_i C_j}, \quad (9)$$

which in turn implies that

$$\frac{K_{Ai}}{K_{Bi}} = \frac{K_{Aj}}{K_{Bj}}. \quad (10)$$

Thus, a mixed ESS solution is only possible if the ratio of the efficiencies of the two phenotypes is the same on each patch.

In order to find this ESS solution we define two constants:

$$R = \frac{Q_i}{Q_j} \quad (11)$$

$$M = \frac{K_{Ai}}{K_{Aj}} = \frac{K_{Bi}}{K_{Bj}} \quad (12)$$

This allows (8) to be rewritten as

$$\frac{C_i}{C_j} = RM. \quad (13)$$

In order to find the ESS in terms of the proportion of A individuals on patch p we need to rearrange (13) to give p_{Ai} in terms of p_{Bi} . Substituting from equations (1) – (4) into (13), and after some algebraic manipulation, we obtain:

$$p_{Ai} = \frac{-P_B p_{Bi}}{P_A} + \frac{RM(P_A + P_B)}{P_A(1 + RM)}. \quad (14)$$

Now we can see that any pair $\{p_{Ai}, p_{Bi}\}$ which satisfies this, and which satisfies

$$0 \leq p_{Ai}; p_{Bi} \leq 1, \quad (15)$$

is an ESS solution. This can be summarised as any point where the straight line in Fig. 6.1 intersects the shaded box.

We now explore the types of ESS distributions that are possible for various combinations of values for the parameters R , M , P_A and P_B .

From Fig. 6.1, it is easy to see that mixed ESS distributions will be present, providing that the value of p_{Ai} given by equation (14) is less than one when $p_{Bi} = 1$. From (14) this translates into the condition

$$\frac{RM}{1 + RM} - \frac{P_B}{P_A(1 + RM)} < 1. \quad (16)$$

Since all four parameters have values greater than zero, this case is always satisfied. Hence, there are always mixed solutions.

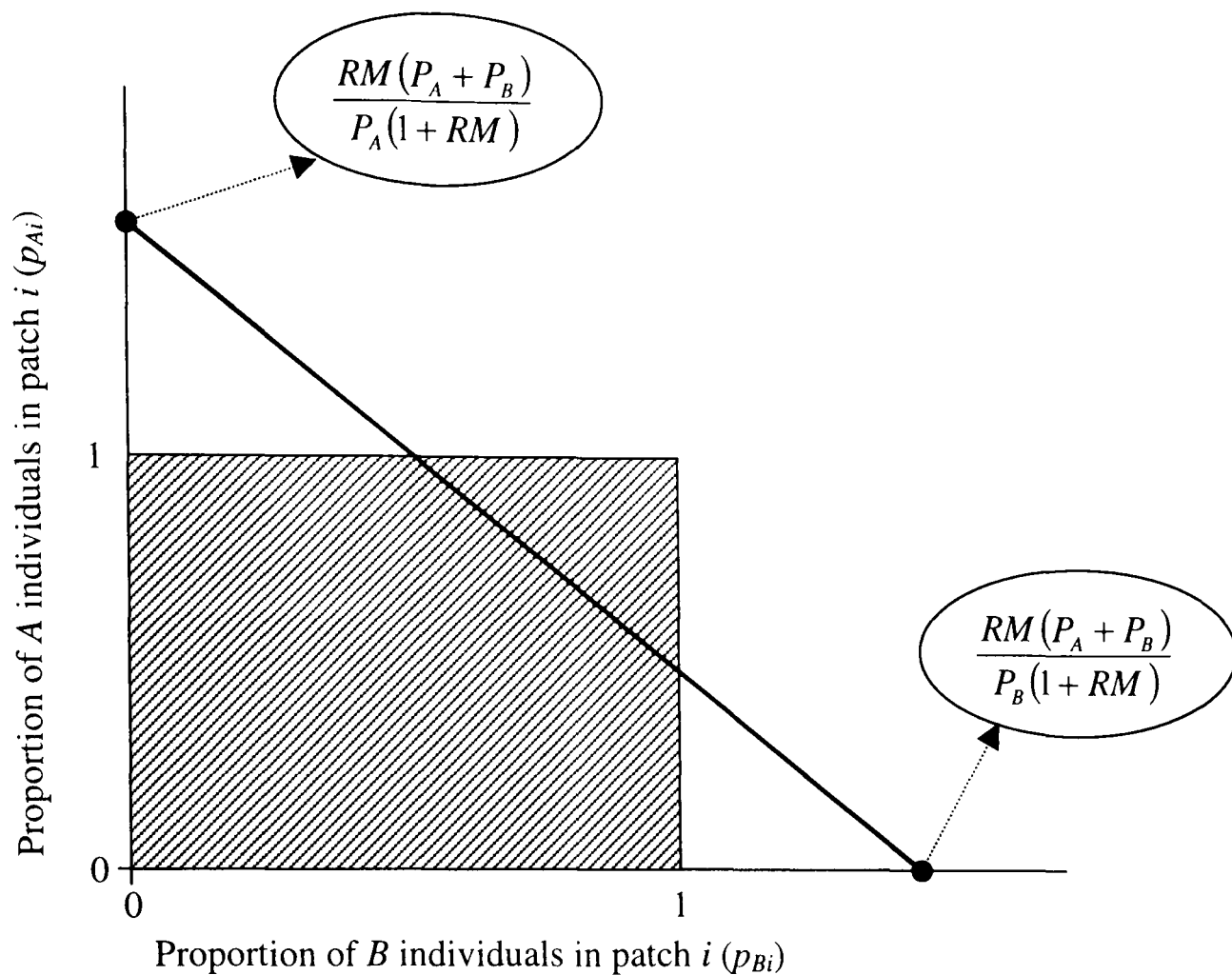


Figure 6.1. Graphical description of equation (14). All combinations of p_{Ai} and p_{Bi} where the diagonal line intersects the shaded box are ESS solutions. Note that the line representing eqn. (14) may intersect either axis at any point above or below the value 1.

We now look for non-mixed solutions where at least one of the two phenotypes is confined to one patch. There are three possibilities: phenotype A may be confined to one patch whilst B is not; phenotype B may be confined to one patch whilst A is not (we refer to these as partially segregated distributions); or phenotype A may be confined to one patch whilst B is confined to the other (we refer to this as a fully segregated distribution). We begin by looking for solutions where phenotype A is confined to one patch. Without loss of generality we can arbitrarily define this patch as patch i . From Fig. 6.1 we can see that such solutions exist providing we satisfy the condition

$$\frac{RM(P_A + P_B)}{P_A(1 + RM)} > 1 \quad (17)$$

It can be seen that this is more likely to be satisfied if $P_B \gg P_A$, which stands to reason: if A individuals dominate the total population, it is unlikely that they would maximise their fitness if they only exploited one patch. This condition is also more likely to be satisfied if RM is large, which means that patch i is relatively more productive than patch j and that individuals have a higher resource to energy conversion efficiency on patch i than j .

Similarly, the condition for a solution to exist where all individuals of phenotype A are confined to patch j is

$$\frac{RM(P_A + P_B)}{P_B(1 + RM)} < 1. \quad (18)$$

It is clear that this is most likely to be satisfied when there are many more individuals of phenotype B than A , and when RM is small, which means that patch j is relatively more productive than patch i and that individuals have a higher resource to energy conversion efficiency on patch j than on i .

By similar reasoning, it is easy to show that a solution will exist with individuals of phenotype B confined to patch i

$$\frac{RM(P_A + P_B)}{P_B(1 + RM)} > 1. \quad (19)$$

and for the solution where all the B individuals are confined to patch j , we require:

$$\frac{RM(P_A + P_B)}{P_A(1 + RM)} < 1. \quad (20)$$

Finally, the solution where all the B individuals are on patch i and all the A individuals are on patch j is

$$\frac{RM(P_A + P_B)}{P_B(1 + RM)} = 1. \quad (21)$$

Conversely, the solution where all the B individuals are on patch j whilst all the A individuals are on patch i is

$$\frac{RM(P_A + P_B)}{P_A(1 + RM)} = 1. \quad (22)$$

In summary, when the relative efficiencies of phenotypes are the same on both patches, for all combinations of parameter values, a continuum of mixed ESS distributions exists in combination with two distributions where at least one phenotype is confined to one patch (semi-segregated distributions). Fully segregated distributions (where both phenotypes are confined to different patches) can only occur for very specific combinations of parameter values and hence are very unlikely to have any ecological relevance.

Differing efficiencies

We now turn to the case where the relative efficiencies of phenotypes differ between patches. Specifically we define

$$K = \frac{K_{Ai}}{K_{Aj}}, \text{ and } \frac{K_{Bi}}{K_{Bj}} = L, \text{ therefore } K > L \quad (23)$$

We know that for $K \neq L$, no mixed ESS distributions exist. In the appendix, we show that for any set of parameter values, there is only ever one ESS distribution. Specifically, there are three possible situations, as shown in Fig. 6.2. For any of these solutions the equilibrium distribution may be fully or partially segregated, but it will never be mixed. That is, at least one phenotype is always restricted to a single patch. This is markedly different from the traditionally studied case with $K = L$, where for any combination of parameter values there will be a distribution of alternative ESS solutions, almost all of which will be mixed (see Sutherland & Parker 1985, 1992, Parker & Sutherland 1986, and equations (11) to (16))

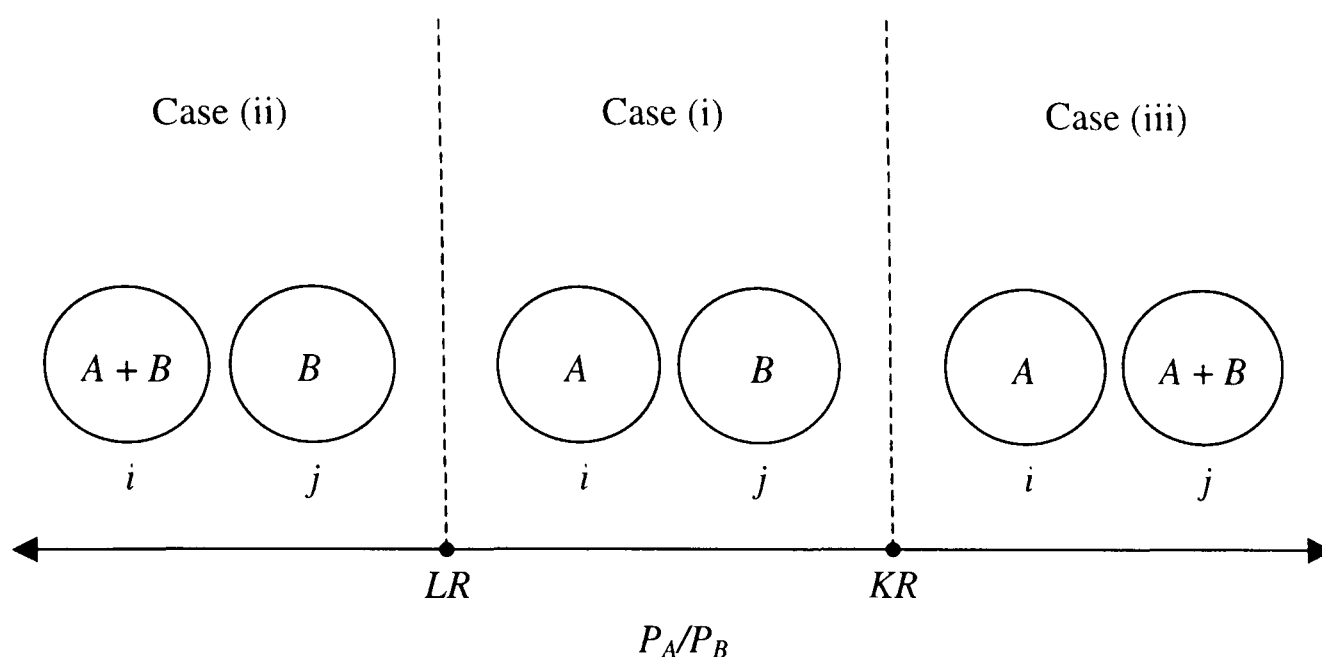


Figure 6.2. For the case where $K \neq L$ only one equilibrium distribution is possible for any given set of parameter values. In case (i), where the ratio of P_A/P_B falls between LR and KR , the resultant distribution is an ESS where all individuals are fully segregated, i.e. all individuals of phenotype A are confined to patch i whilst all those of phenotype B are confined to patch j . In case (ii), where the ratio of P_A/P_B is less than LR , individuals of phenotype A are confined to patch i whilst individuals of phenotype B are mixed between the two patches. Conversely, in case (iii), where the ratio of P_A/P_B is greater than KR , individuals of phenotype B are confined to patch j whilst individuals of phenotype A are mixed between the two patches.

Discussion

The concept of post-acquisitional phenotypic differences is, to our knowledge, an unexplored aspect of IFD theory. Our analytical conclusions indicate that these differences can have dramatic and important effects on expected distributions of otherwise equal competitors. Previous models that have dealt with unequal competitors (e.g. Sutherland & Parker 1985, Sutherland & Parker 1992, Parker & Sutherland 1986) tend to make the prediction that there will be multiple equilibrium distributions, the exact form of which depends upon starting conditions (but see also Korona 1989 and Tregenza 1995 for a review). Our model, however, predicts a continuum of ESS distributions, in combination with two semi-segregated distributions. Fully segregated distributions (i.e. truncated phenotype distributions where both phenotypes are confined to different patches) can also occur, but only for specific and biologically unlikely parameter combinations.

The few models that consider differential relative competitive ability between patches (e.g. Parker 1982, Parker & Sutherland 1986, Sutherland & Parker 1992) produce predictions that have a strong commonality to those presented here for differences in post-acquisitional traits. Both models predict that when the relative advantage of the trait under consideration differs between patches, there will only ever be one ESS at equilibrium. This distribution may be fully or partially segregated, but it will never be mixed. Therefore, it is clear that, in terms of resultant stable distributions, it does not matter whether individual differences are expressed before or after competition for resources. Unquestionably, post-acquisitional differences should now be considered as equally important determinants of the distribution of animals in their environment as competitive differences currently are. Further, the implicit assumption in many models that the relative abilities of individuals are independent of the context of their interaction must be re-examined. Both our work and that of Parker (1982) conclude that any deviation from this strict assumption leads to fundamentally very different model predictions.

Our results have far reaching consequences for our understanding of the way animals distribute themselves between resources. They illustrate the need for empirical examination of how both the competitive ability and post-acquisitional efficiency of individuals differ between situations. However, our work considers only two phenotypes, and there is clearly a need for more theoretical work to examine how our results generalise for both multiple phenotypes and multiple patches. The distributions discussed here are not limited to single populations or even species. IFD models have been used by several authors to explain distributions and niche separation of competing species (e.g. Rosenzweig 1981). We suggest that non-competitive differences between species may help explain some of the segregation of potentially competing species within their environments. Our model may be particularly important in studies of non-native invasions where populations at the edge of their range overlap in certain habitats but not others.

In summary, differences between phenotypes in traits other than those involved with direct competition may be more important to the distributions of those phenotypes than has previously been suspected. We suggest that further examination of the

consequences of post-acquisitional phenotypic differences is likely to yield many more predictions and will increase our understanding of resource partitioning at many levels from individual to species differences.

Appendix: Derivation of ESS distributions when relative efficiencies differ between patches.

From equation (23) we have

$$K = \frac{K_{Ai}}{K_{Aj}} > \frac{K_{Bi}}{K_{Bj}} = L \quad (\text{A1})$$

We know that for $K \neq L$, no mixed ESS distributions exist. Hence, we will explore the conditions required for other ESSs to exist. We consider three alternatives: because of the assumption that $K > L$, we expect A individuals to have a preference for patch i and, consequently, B individuals to have a preference for patch j . Hence the three types of non-mixed solutions that we need to consider are as follows:

- i) all of phenotype A on one patch and all of phenotype B on the other
- ii) all of phenotype A on one patch, but phenotype B occurring on both patches
- iii) all of phenotype B on one patch, but phenotype A occurring on both patches

Case (i)

Without loss of generality, we look for a solution where all A individuals are on patch i and all B individuals on patch j . Thus, we can ask, under what conditions is $\{p_{Ai}, p_{Bi}\} = \{1, 0\}$ an ESS?

For this, the reward rate of an A individual must decrease if it moves to patch j . This translates into the condition

$$\frac{K_{Ai}Q_i}{P_A} > \frac{K_{Aj}Q_j}{P_B + 1} \quad (\text{A2})$$

Since we are assuming that the population sizes of both phenotypes are very large, we can effectively approximate this by

$$\frac{K_{Ai}Q_i}{P_A} > \frac{K_{Aj}Q_j}{P_B}. \quad (\text{A3})$$

Using (11) and (12), this can be rearranged to give

$$KR > \frac{P_A}{P_B}. \quad (\text{A4})$$

We can see that this condition is easiest to satisfy when the population size of phenotype A is small (compared to that of phenotype B), when resources arrive at a greater rate on patch i than on patch j , and when the exploitative efficiency of phenotype A is stronger on patch i than on patch j . All of which are in accordance with intuition.

The other condition for $\{1,0\}$ to be an ESS is that the reward rate of a B individual should decrease if it moves to patch i . This translates into the condition

$$\frac{K_{Bj}Q_j}{P_B} > \frac{K_{Bi}Q_i}{P_A + 1}. \quad (\text{A5})$$

Using (11) and (12), and making the “large population size” approximation, this can be rearranged to give

$$LR < \frac{P_A}{P_B}. \quad (\text{A6})$$

In contrast to (A4) we can see that this condition is easiest to satisfy when the population size of phenotype A is large (compared to that of phenotype B), when resources arrive at a *lower* rate on patch i than one patch j , and when the exploitative efficiency of phenotype B is stronger on patch i than on patch j .

Considering both of these conditions, we find that the total segregated distribution $\{1,0\}$ will be an ESS whenever we satisfy

$$KR > \frac{P_A}{P_B} > LR. \quad (\text{A7})$$

Case (ii)

We now turn our attention to partially segregated solutions where all of the A individuals are on patch i , but the B individuals are spread between both patches such that a fraction β of them are on patch i . That is, when will $\{1, 0 < \beta < 1\}$ be an ESS?

Using the large populations assumption, the condition for no B individual to want to move is that at equilibrium, the reward rate for all B individuals is the same in both patches:

$$\frac{Q_i K_{Bi}}{P_A + \beta P_B} = \frac{Q_j K_{Bj}}{(1 - \beta)P_B}. \quad (\text{A8})$$

This can be rearranged to give an expression for β :

$$\beta = \frac{RLP_B - P_A}{P_B(1 + RL)}. \quad (\text{A9})$$

The condition that $\beta > 0$ now becomes

$$RL > \frac{P_A}{P_B}. \quad (\text{A10})$$

In addition, the condition that $\beta < 1$ becomes

$$RLP_B + P_B > RLP_B - P_A, \quad (\text{A11})$$

which is always satisfied.

We also demand that no A individual should increase its resource gain rate by moving to patch j :

$$\frac{Q_i K_{Ai}}{P_A + \beta P_B} > \frac{Q_j K_{Aj}}{(1 - \beta) P_B}. \quad (\text{A12})$$

Using (A9), this simplifies to

$$K > L, \quad (\text{A13})$$

which is no real restriction, as this assumption has already been made. Therefore, the only condition for $\{1, 0 < \beta < 1\}$ to be an ESS is that

$$RL > \frac{P_A}{P_B}. \quad (\text{A14})$$

If we compare this condition with (A7), we find that partially segregated solutions of the form $\{1, 0 < \beta < 1\}$ can never be stable when the full segregated solution $\{1, 0\}$ is stable. Further, whenever the ratio of the number of A individuals to the number of B individuals is too low for $\{1, 0\}$ to be an ESS, there is always a single partially segregated solution of the form $\{1, 0 < \beta < 1\}$ which is stable.

Case (iii)

We now consider the alternative partially segregated solutions where all the B individuals are on patch j , but the A individuals are spread between both patches such that a fraction α of them are on patch i . That is, we ask, when will $\{0 < \alpha < 1, 0\}$ be an ESS?

Using the large populations assumption, at equilibrium the reward rate for A individuals is the same in both patches

$$\frac{Q_i K_{Ai}}{\alpha P_A} = \frac{Q_j K_{Aj}}{P_B + (1-\alpha)P_A}. \quad (\text{A15})$$

This can be rearranged to give an expression for α :

$$\alpha = \frac{RK(P_A + P_B)}{P_A(1 + RK)}. \quad (\text{A16})$$

By inspection, we can see that the condition $\alpha > 0$ will always be satisfied. The condition that $\alpha < 1$ now becomes

$$RK < \frac{P_A}{P_B}. \quad (\text{A17})$$

We also demand that no B individual will increase its resource gain rate by moving to patch i :

$$\frac{Q_j K_{Bj}}{P_B + (1-\alpha)P_A} > \frac{Q_i K_{Bi}}{\alpha P_A}, \quad (\text{A18})$$

which simplifies to

$$K > L, \quad (\text{A19})$$

Again, this assumption has already been made, meaning that this inequality is not an important restriction. Hence, the only condition for $\{0 < \alpha < 1, 0\}$ to be an ESS is that

$$RK < \frac{P_A}{P_B}. \quad (\text{A20})$$

Again, if we compare this condition with (A7), we find that partially segregated solutions of the form $\{0 < \alpha < 1, 0\}$ can never be evolutionarily stable when the full

segregated solution $\{1,0\}$ is stable. Nevertheless, whenever the ratio of the number of A individuals to the number of B individuals is too high for $\{1,0\}$ to be an ESS, there is always a single partially segregated solution of the form $\{0 < \alpha < 1, 0\}$ which is stable.

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MULTIPLE IDEAL FREE DISTRIBUTIONS OF UNEQUAL COMPETITORS

Abstract

We study an individual-based model of a number of competitors each able to move freely between two resources. If individuals move only so as to improve their resource gathering rate, then the system settles to one of a finite number of equilibria (often called ideal free distributions). The addition of occasional switching of a randomly selected individual between resources does not (contrary to the predictions of Hugie & Grand 1998) lead to this distribution of equilibria collapsing to a single point. In fact, it can induce the population to periodically shift between equilibria, thereby increasing spatio-temporal variation in competitor numbers. We further show that the probability of the system reaching a given equilibrium is critically dependent on the fine detail of the rules describing individual movements.

Introduction

Ideal free distribution (IFD) theory describes how animals should be distributed between a number of resources such that none would benefit by switching between resources. A key prediction of IFD theory is that if individuals differ in competitive ability, then for a given resource distribution, several different equilibrium distributions of animals are possible (Houston & McNamara 1988, Milinski & Parker 1991). That is, there will be several alternative distributions of a given set of animals such that none can improve their resource acquisition rate by unilaterally moving to another patch. Recently however, Hugie and Grand (1998) have suggested that the addition of movements of individuals for reasons other than maximising resource acquisition rate has a profound effect on such systems, such that now only a single stable distribution occurs. Our aim in this paper is to explore the validity and generality of this important and iconoclastic suggestion.

Hugie and Grand (1998) use a differential equation description of movement rates between patches. An implicit assumption made in adopting such a formulation is that population numbers are sufficiently high that the stochastic nature of individual movements can be ignored (see Wilson 1998 for a careful discussion of this). Since most experimental tests of IFD theory (see Table 1 of Hugie & Grand 1998) use fewer (normally considerably fewer) than 100 individuals, we have chosen not to make this assumption, but rather to construct an individual-based model which records each movement separately. However, in other respects the underlying assumptions of our model are identical to those of Hugie and Grand (1998), allowing comparisons to be made. We define the model in the next section.

The model

Our environment consists of two habitats: the “good” one produces resources at twice the rate of the “poor” one. The population of animals consists of 72 individuals each with a defined competitive weight. Thirty-six “good” individuals all have an identical competitive weight, which is twice as good as the 36 identical “poor” competitors. Each individual’s harvesting rate is the product of the resource production rate of the habitat that they are in, multiplied by their competitive weight.

and then divided by the total of the competitive weights of all individuals in that habitat. Each simulation starts with every individual randomly and independently assigned to one of the two environments. There then follows 10,000 “turns” each consisting of an opportunity for a single non-IFD movement followed by an opportunity for an IFD one.

Each time there is an opportunity for a non-IFD movement, a uniform random number between zero and one is drawn. If this number is below a constant value Q , then a non-IFD movement occurs. This involves one of the 72 individuals being chosen at random and moved to the other habitat.

Each time there is an opportunity for an IFD movement, the set of individuals that would improve their harvest rate if they unilaterally moved to the other habitat is constructed. An individual from this set is selected, and moved to the other patch. This individual is selected in one of three ways:

- i) randomly,
- ii) such that the individual which will improve its harvesting rate the most is selected,
- iii) such that the individual which currently has the lowest harvesting rate is selected.

In cases (ii) and (iii), if the rule selects not a unique individual but a subset, then one individual from the subset is chosen randomly.

Model predictions

Consider the case where we use the random movement rule (i) and have no non-IFD movement ($Q=0$). Then the results of 10,000 simulations (each using a different random number sequence) are given in the first diagram of Figure 7.1. Each simulation quickly settles down to an equilibrium where the ratio of the total competitive weights in each habitat is the same as the ratio of patch resource production rates (i.e. 2:1). Theoretically, this can be achieved in 18 different ways: the good patch could hold only the 36 good individuals, or 35 good individuals and 2

poor ones, or 34 good and 4 poor, and so on to the distribution with 18 good and 36 poor individuals. The distribution which any one simulation settles to will be a function of the randomly generated initial distribution and the order in which individuals move. We see that in this case the most commonly observed equilibrium is that with 24 good (and so 24 poor) competitors in the good patch, and that equilibria with either a very high or very low number of good competitors in the good patch are very rare (in fact some never occurred in 10,000 simulations). These predictions are in accord with the established theory of Houston and McNamara (1988) for unequal competitors. The theory of Hugie and Grand (1998) suggests that if we now add non-IFD movements to the simulations then we will no longer observe this distribution of alternative equilibria; rather the system will always converge to the same unique equilibrium. In fact, as can be seen in Figure 7.1, regardless of the frequency of non-IFD movements (i.e. the value of Q), we still find that the number of good competitors in a patch can vary considerably between simulations. When Q is low, then the occurrence of a non-IFD movement is quickly followed by a succession of IFD movements, which move the system back to one of the IFD equilibria (not necessarily the same one as before the non-IFD movement), where it will sit until the next non-IFD movement. Hence, the system spends most of its time sitting in one or other of the equilibria. When Q is higher, the probability of a further non-IFD movement occurring before a series of IFD movements has returned the system to an equilibrium is increased, and so the system spends more time away from the equilibria. Furthermore, as Figure 7.2 illustrates, even low occurrences of non-IFD movement can lead to considerable variation in the distribution of individuals within a single simulation. These observations still hold true, if we use the alternative rules for selecting individuals for IFD movements (Figures 7.1 & 7.3).

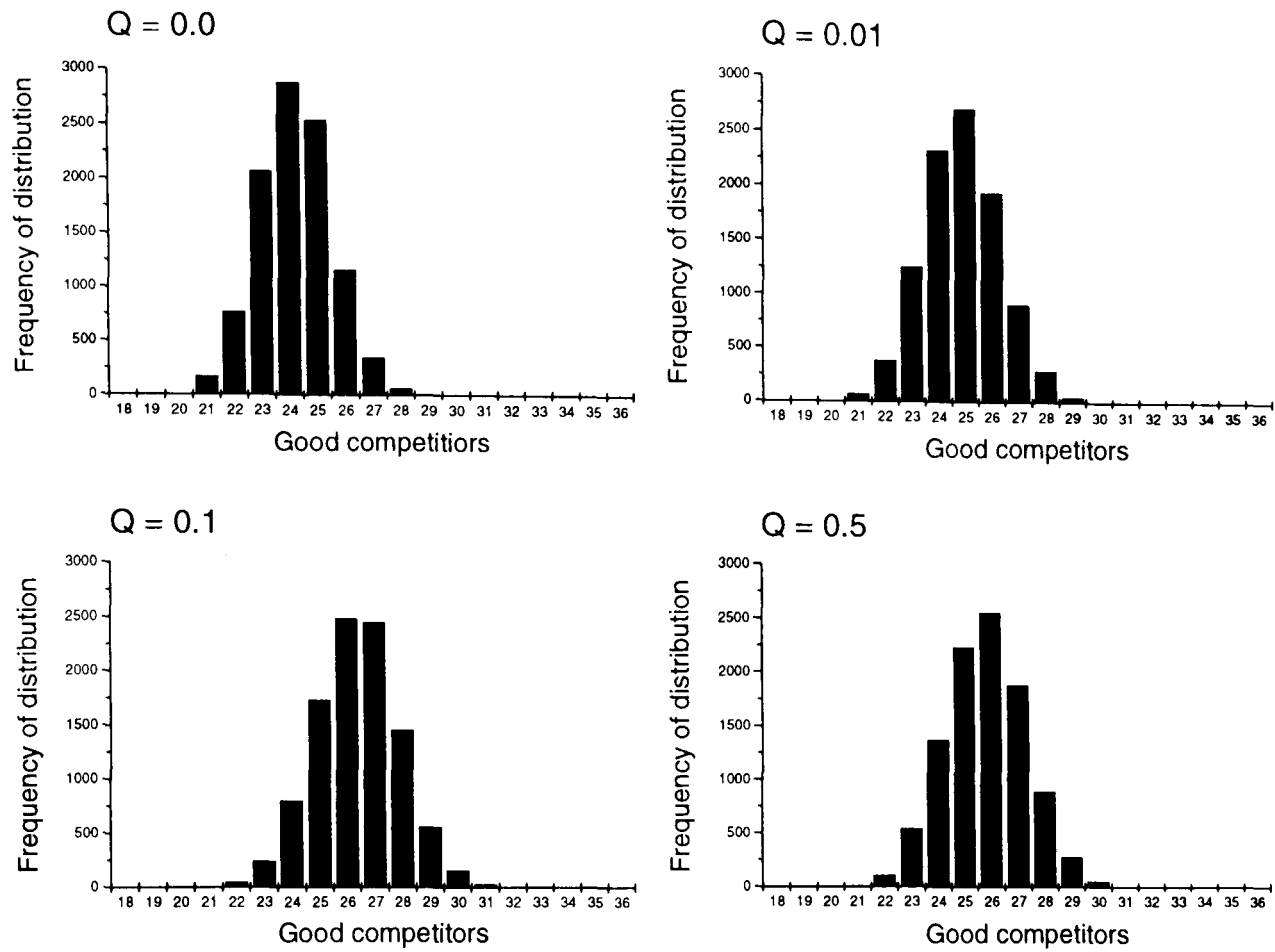


Figure 7.1: The model was run with random selection of IFD movers (case i) for 10000 simulations each differing only in the sequence of random numbers used. In each simulation the number of good competitors in the good patch after 10000 turns was recorded. The distribution of these numbers is shown for four situations: with $Q = 0, 0.01, 0.1$ and 0.5 . For $Q > 0$, we see considerable variation between simulations, contrary to the predictions of Hugie & Grand (1998).

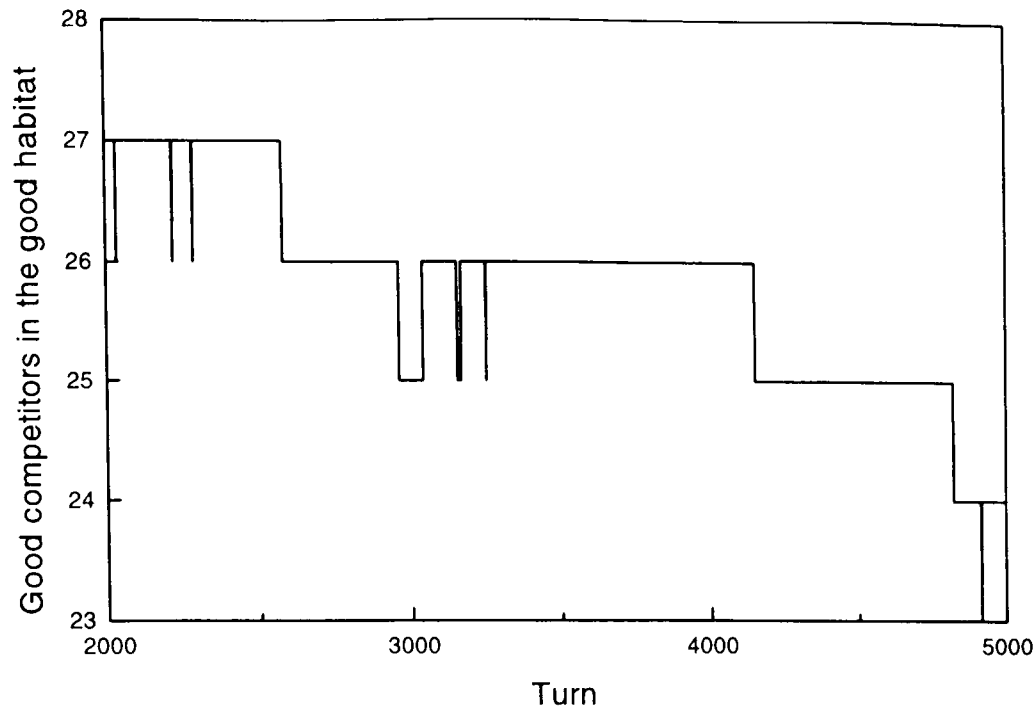


Figure 7.2: Time series showing the number of good individuals in the good patch for part of one simulation with movement case i and $Q = 0.01$. Although the system can spend long periods sitting at an equilibrium, occasionally non-IFD movements produce shifts between equilibria.

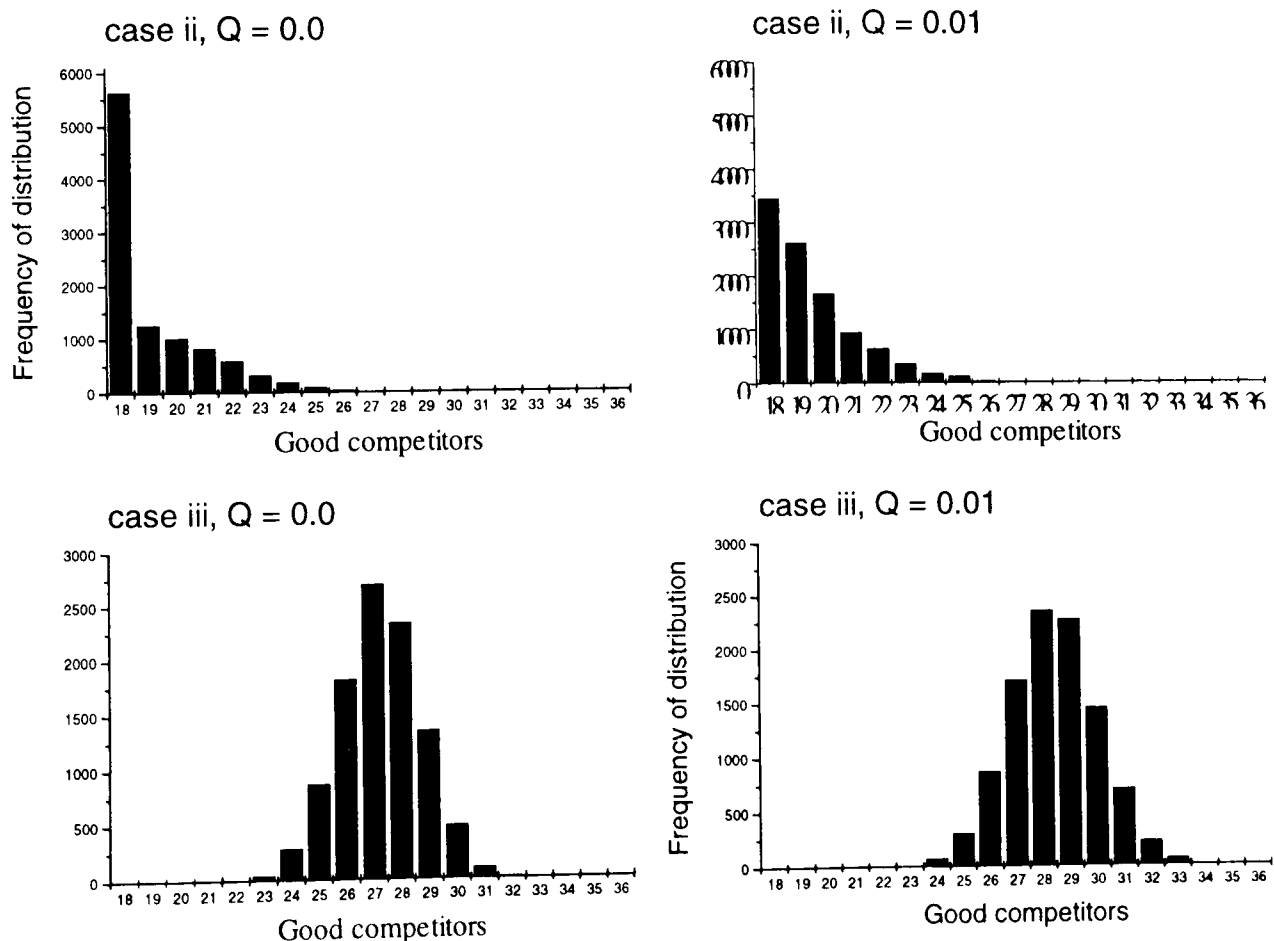


Figure 7.3: The model was run for four sets of 10000 simulations. In each simulation the number of good competitors in the good patch after 10000 turns was recorded. The distribution of these numbers is shown for four situations: movement case ii, $Q = 0$; movement case ii, $Q = 0.01$; movement case iii, $Q = 0$; and movement case iii, $Q = 0.01$. In each case, we see considerable variation between simulations, and a strong effect of movement rule.

Discussion

Our simulations do not agree with the conclusions of Hugie and Grand (1998): we find no evidence that the introduction of non-IFD movement to an individual-based IFD model leads to the creation of a unique equilibrium distribution. Further, this may not be related solely to the effects of stochasticity resulting from the small number of individuals in our model. Even for the deterministic large-population limit that they consider, we believe that they have misinterpreted their analysis. They state that, “it can be shown that a single, stable distribution of each competitor type will always occur (see Appendix), corresponding to a single equilibrium point” (Hugie and Grand 1998). In fact, the Appendix does not demonstrate anything about the number of possible equilibria; all it shows is that any possible equilibria will be locally stable against infinitely small perturbations. However, our contention is that (as for the simple case with no non-IFD movements) their full model will have no single unique equilibrium, but a distribution of equilibria. This distribution could be represented by a single line in parameter space defined by orthogonal axes each of which is the fraction of a given phenotype in a given habitat.

However, this important reinterpretation notwithstanding, the work of Hugie and Grand (1998) should make an important contribution to foraging theory if it causes ecologists to reconsider the importance of non-IFD movements. Such movements are likely to occur in many systems, simply through mistakes, sampling behaviour, or for reasons not directly connected with resource acquisition (such as a risk of predation or mating opportunities). We have shown here that non-IFD movements may have a profound ecological importance. As Figure 7.2 demonstrates, even when rare, non-IFD movements can have a considerable impact on the spatio-temporal distribution of individuals across habitats. Sometimes a single non-IFD movement can trigger a cascade of IFD movements that move the system from one equilibrium to a wholly different one. Hence non-IFD movements may lead to an increase in the temporal variance of the population density exploiting a given habitat. Further, this effect may be pronounced even when non-IFD movements are rare.

Lastly, comparison of Figures 7.1 and 7.3 demonstrates that small perturbations to the rules underlying the movement of individuals between patches can have a profound impact on the relative likelihood of the system settling on different equilibria. Similar observations of the sensitivity of systems to the order in which individuals begin to exploit the habitats (a consideration ignored in our study) have recently been made by Houston & Lang (1998).

Acknowledgements

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**MODELLING TERRITORIAL BEHAVIOUR OF ANIMALS IN VARIABLE
ENVIRONMENTS**

Abstract

We present an individual-based model describing the distribution and resource gain of territorial individuals in situations where the rank order of territory quality changes over time. The model integrates both competitive (territory holding ability) asymmetries and a memory function. Results indicate that there is a balance of effects resulting in a peak in movement rates, but not resource gain, for individuals of intermediate ability. Furthermore, when the system is reduced to a linear array of territories (as commonly used in empirical studies) the model generates quite different predictions because of the severe limitation in movement that the linear array imposes. We suggest that the model can be used to generate testable predictions for territorial species such as salmonids, and that future empirical work should take into account the consequences of reductions in movement imposed by a linear array of territories.

Introduction

Relationships between the distributions of animals, the distributions of resources useful to them, and the rates at which they utilise these resources can be powerful tools for investigating population processes in terms of the behaviour of individuals (Sutherland 1996). Most such models build on the Ideal Free Distribution (hereafter IFD, Fretwell & Lucas 1970, Fretwell 1972). In an IFD, individual animals are equal in their competitive abilities, are free to move between resource patches, and have perfect knowledge of the qualities of all available patches. Under such circumstances there is perfect matching between the quality of a patch and the number of animals that use it, such that no individual can improve its rate of resource acquisition by moving. For real animals, the situation is more complex, and much attention has been given to elaborating the model to include more realistic assumptions (e.g. Bernstein *et al.* 1988 and references therein, Tregenza 1995). However, the IFD is not well suited to modelling behaviour and population distributions of territorial animals, where some individuals restrict the access of others to resources.

Fretwell (1972) developed the Ideal Despotic Distribution (hereafter IDD) to predict the distributions of territorial birds settling in a habitat. In this model, each animal arriving in a habitat can assess the value of patches but is not free to use areas that are already occupied. Thus, there are essentially two commonly used approaches to modelling patch choice by animals. Whilst the IFD has been developed and applied widely, this has not been the case for the IDD (Milinski & Parker 1991) despite the fact that interference between individuals (acting as a constraint on their ability to search) is likely to be common in many natural situations (e.g. Armstrong *et al.* 1997, Hall & Fedigan 1997). However, as Tregenza (1995) points out, in its simplest form, the IDD's only prediction not common to the IFD is that territory ownership will lead to differential success of otherwise equal competitors. A lack of alternative models has probably led to the IDD being cited as an important predictor of despotic distributions simply because it comes closer to predicting observed distributions than the IFD (Tregenza 1995).

One reason why the IDD is not more widely used is that in many cases its outcomes are intuitively obvious. For example, if we rank habitat patches in order of quality and rank individual animals in order of competitive ability (henceforth termed "dominance") then we might expect a simple matching between dominance rank and patch quality. Such a simple intuitive model is appropriate for systems where there is little or no change in the relative quality of different sites, e.g. salmonid fishes occupying territories in river pools where more food is available at the heads than at the tails of pools (Nakano 1995, Hughes 1992). However, not all natural environments are predictable in time and space in this way. For example, in shallow riffle river habitats the relative qualities of adjacent habitat patches vary continually and ranks of patches are not stable (JD Armstrong unpublished data). When relative patch qualities change rapidly, neither the IFD nor the IDD are appropriate representations of patterns of patch exploitation. New methodologies, which take into account the finite ability of individuals to respond to rapid change in their environment, must be developed. Here we use an individual-based model together with an optimisation approach to explore how habitat heterogeneity affects movement and energy intake rates of animals in a hierarchy of competitive ability. This model allows us to examine the effects of foragers having limited knowledge, in terms of constrained movements and imperfect memory, in contrast to the 'ideal' foragers considered by the IFD and IDD. We describe how this basic model influences patterns of movement and resource gain of individual animals within such populations.

The model

We use an individual-based model with a number of competitors N . Each of these has an intrinsic and unique rank R_i , which is constant over time, labelled such that low numbered rank equates with high competitive ability. Each individual also has an intrinsic estimate (E_i) of the (long-term) average reward rate that it expects to be able to harvest. This estimate is dynamic and is constantly updated by incorporating information about the actual reward rate obtained by the individual. The environment consists of an $L \times L$ square matrix of territories. At any point in time, each of the territories is characterised by the resource production rate $E_{x,y,t}$ that can be harvested

by an individual holding that territory. This production rate will vary both between territories at any given time, and over time in any given territory. Although several individuals can be sited in the same territory, only the highest ranked one receives reward from the territory.

A simulation begins with each individual randomly assigned to a territory, and assigned a starting foraging expectation of E_i . Each territory is assigned a resource production rate drawn (independently) from a normal distribution with mean μ and standard deviation σ . *Time* (the total length of the simulation) is divided into equal intervals of length Δ . Each of these time intervals consists of two phases: change in the environment followed by movement of individuals in response to that change.

We assume that the probability (per unit time) of the resource production rate of a given territory changing is a constant (C). Hence, during each time interval of length Δ , the probability that the given territory changes is given by the product $C\Delta$. At the start of every time interval, the value of each of the territories is changed independently with that probability; each new resource production rate being drawn (independently) from the same normal distribution that was used to produce the initial values.

After each round of environmental change, each of the N individuals is considered in turn (in random order): If the reward rate on its current territory (which is a function both of the resource production rate of that territory and of the relative rankings of any other individuals in the territory) is higher than the individual's expectation E_i , then it stays in the territory. Otherwise it moves to an adjacent territory (chosen at random) from the subset of neighbouring territories containing no individuals or only individuals of lower rank. If none of the neighbouring territories meets these criteria, then the individual remains where it is. Implicitly, we assume that individuals cannot estimate the resource production rate of neighbouring territories, but that they can detect the rank of any individual in those territories. We can interpret Δ as the time required to assess the quality of a newly-entered territory. If such an "environmentally-triggered" move results in an individual moving to a territory

which contains lower ranked individuals, then this has a detrimental effect on the highest ranking of these (i.e. it loses possession of the territory). In such cases, this individual attempts to move to an adjacent territory (choosing from its neighbours in exactly the same way as described above). This “invasion-triggered” movement could result in yet another individual losing possession of a territory, in which case a cascade of invasion-triggered movements occurs. When such a cascade finishes, with an individual moving to a previously unoccupied territory or remaining where it is (because none of the neighbouring territories are suitable), we return to considering the remaining individuals for environmentally-triggered movement. This model of movement has strong similarities with the biased diffusion models used recently by Farnsworth and Beecham (1997) to explore aspects of the IFD.

After each individual has been allowed to make one environmentally-triggered move (if appropriate), each receives a reward F , which is either equal to the resource production rate of its current site $E_{i,j,t}$ multiplied by Δ (if it is the highest ranked individual on that site), or zero (otherwise). Each individual then updates its expected foraging return E_i according to the equation

$$E_i(\text{new}) = \alpha F + (1 - \alpha)E_i(\text{old}),$$

where α is a constant between zero and one; the higher α , the more quickly the individual discounts previous experience. After this, we begin the next time interval.

Model predictions

The model was run with the parameter values indicated in Table 8.1 as default, and only a single parameter was varied in any set of simulations. For each simulation *Time* was set to 10000 and, as Δ was always set to 1.0, the simulation lasted for 10000 repetitions. The results of the simulations are expressed as mean values for each individual’s gain and movement rates, both per unit time. These means are calculated from the last 5000 time intervals only, in order to allow individuals’ expectations to stabilise and the effect of initial conditions to be lost.

The model was run with a variety of different parameter values in order to determine how the uptake and movement rates of individuals of different ranks changed with rank. We were interested in how the results were affected by the following seven parameters

- i) the competitor density, N/L^2
- ii) the matrix shape
- iii) the mean territory quality, μ
- iv) the amount of variation in territory quality, σ
- v) the rate of turnover of territories, C
- vi) the memory parameter, α
- vii) the initial patch estimation, E_i (*initial*)

The range of values used for each of these parameters is given in Table 8.1.

Table 8.1. Values for the seven parameters manipulated in the simulations

| Parameter | Values |
|--|--|
| Competitor density, N/L^2 (only N given) | 15, 30, 36 , 45, 60, 72 |
| Mean territory quality, μ | 0.1, 1.0, 2.5, 5.0 , 7.5, 15 |
| Amount of variation in territory quality, σ | 0.5, 1.5 , 3.0, 5.0 |
| Memory parameter, α | 0.2, 0.4, 0.6, 0.7 , 0.8 |
| Initial patch estimation, E_i (<i>initial</i>) | 0, 2, 4, 6, 8, 10 |
| Rate of turnover of territories, C | 0.2 , 0.4, 0.6, 0.8, 1.0 |
| Matrix shape, $L \times L$ | 6 \times 6 , 4 \times 9, 3 \times 12, 2 \times 18, 1 \times 36 |

For competitor density (N/L^2), only N values are given as, except in the examination of grid shape, L was always six. Only a single parameter value was changed in each simulation, with all other parameters set to their default values (shown in bold type). One simulation was run for each of the values given.

Competitor density (N/L^2): Fig. 8.1a

Figure 8.1a illustrates the gain rate of individuals of different rank in groups of different size. Notice first that the performance of an individual in a given place in the hierarchy is independent of group size (i.e. is independent of the number of individuals in the environment which are further down the dominance hierarchy). For

example, the gain rate of the third ranking individual is the same in a group of 15 as it is in a group of 72. This is because an individual's access to resources is never restricted by the presence of poorer competitors. Conversely, gain rate declines with reduced competitive ability, since higher-ranking individuals do restrict the access that subordinates have to resources. The non-linear shape of this decline can be explained by careful consideration of the structure of the model. At first (until approximately rank 29 in the example shown), gain rate declines slowly with decreasing competitive ability. This is because dominant individuals restrict access to the best sites, and so they usually manage find patches that they can exploit. However, poorer competitors are frequently unable to reach a patch in which they are dominant, and so often gain nothing from their current site. This effect becomes progressively more acute for individuals further down the hierarchy. It occurs because of the limited motility of individuals: in a given time step they can move only to a neighbouring site containing subordinate animals, a situation which becomes increasingly infrequent as rank decreases. Another consequence of the limited motility of individuals is that very poor quality individuals (specifically those whose place in the dominance hierarchy is more than the number of habitats) are still able to occasionally gain reward from a patch. This contrasts with the classical IDD, in which such individuals would always be excluded from all patches.

Initially, movement rates increase with decreasing competitive ability, however, this trend slows and eventually reverses, so that individuals of intermediate rank move more than those both above and below them in the hierarchy. Again, this can be understood by consideration of the structure of the model. The better an individual's competitive ability, the less likely it is to be usurped from its current patch by another animal. The top-ranked individual will only move as a result of environmental change, not because of competitive exclusion by others. However, forced movements become increasingly common as competitive ability decreases, explaining the initial rise in movement rate with declining competitive ability. This effect is countered by the fact that, because individuals lower down the hierarchy are likely to hold a poor patch or no patch at all, they will suffer fewer displacements. Furthermore, although low-ranking individuals will often "want" to move, because their current gain rate is

zero, they will often be hindered by the presence of dominants in surrounding territories, further reducing their movement rates. The balance of these effects is the dome-shaped curve relating movement and rank.

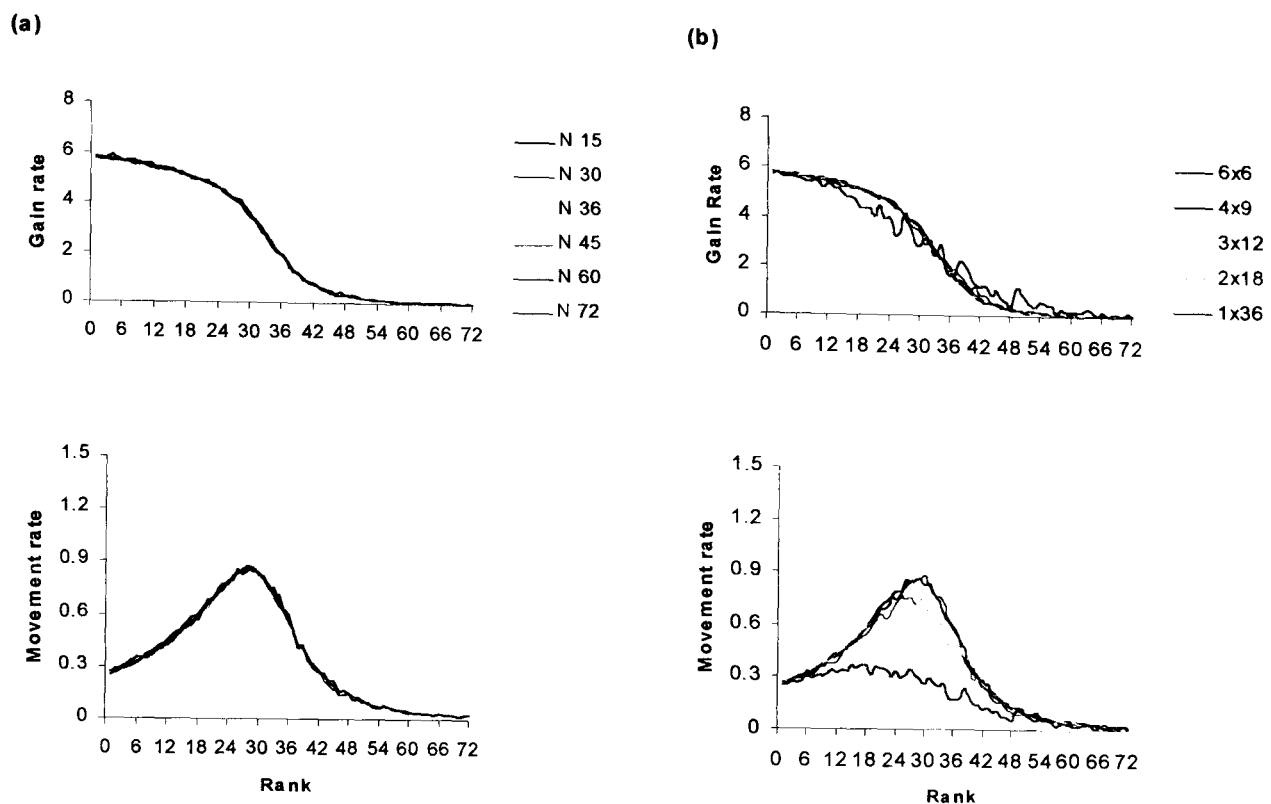


Figure 8.1. Plots of mean gain rate and mean movement rate for manipulation of (a) competitor density and (b) matrix shape. All model parameters not indicated are as given in Table 8.1.

Matrix shape: Fig. 8.1b

The shape of the territory matrix has little effect except in the extreme case of a linear array (1 x 36), which affects both resource gain and movement. There is no effect on the resource gain of top-ranking individuals, but it is reduced in those animals of middle rank and increased in those of very low rank at high densities. This occurs because a linear array greatly constrains the movement choices available to many individuals (they now always have at most two neighbouring sites to choose from), and hence it is very easy for them to become “boxed in” by individuals of higher competitive ability. This effect is felt most strongly by individuals of intermediate dominance rank, which have the highest movement rates (see the explanation of effects of competitor density). Their movement is suppressed markedly in a linear array only one territory wide. The higher rates of resource gain in the lowest ranking animals is due to an increase in the frequency of occasions when they are protected (inadvertently) by high-ranking animals in territories on either side of them.

Mean territory quality (μ): Fig. 8.2a

As expected, all individuals improve their gain rate as the quality of the environment is enhanced by increasing μ . Individuals of higher competitive ability benefit most, as they are best able to exploit the environment. Since we enhance all patches equally, it is unsurprising that this has no substantial effect on movement rates.

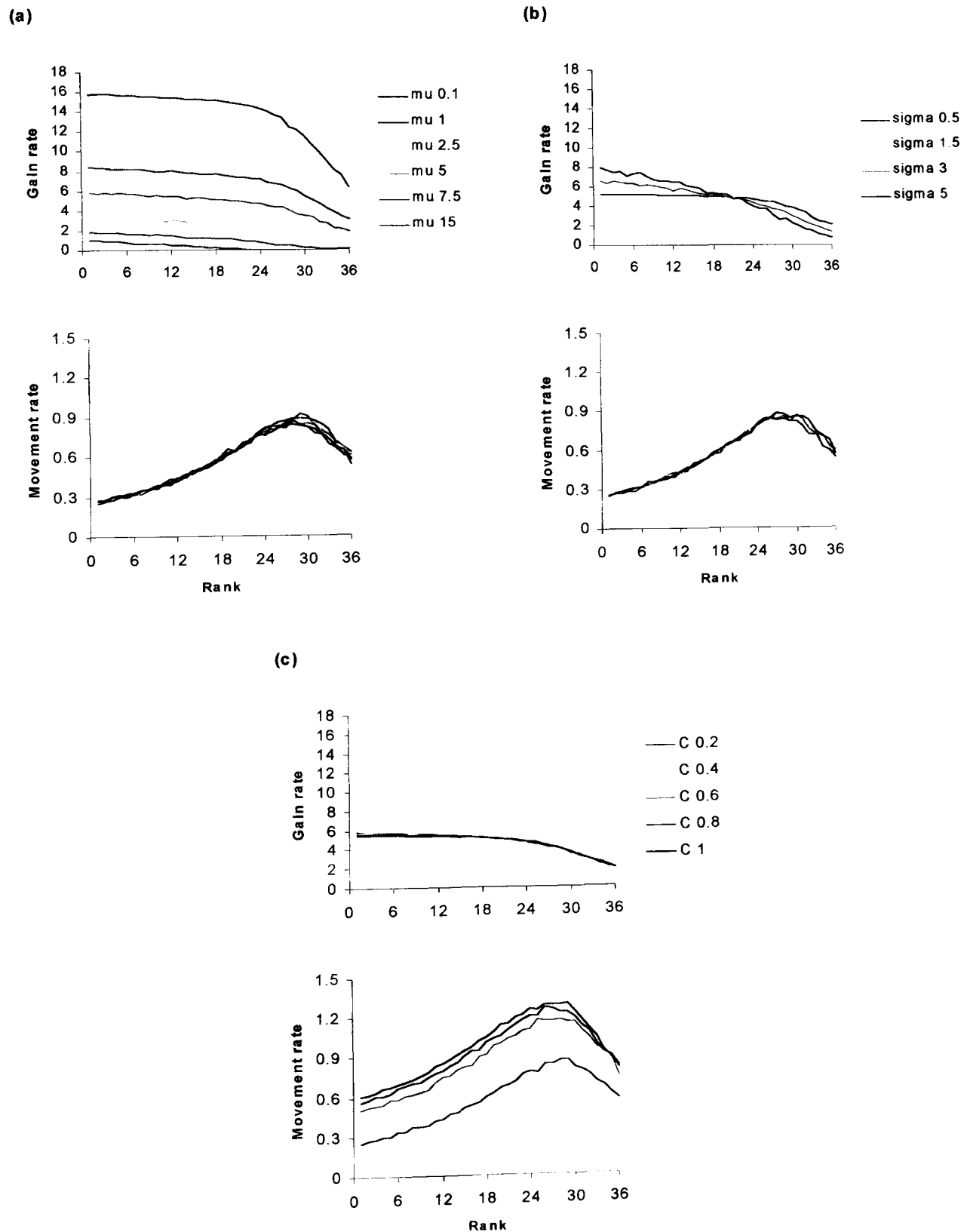


Figure 8.2. Plots of mean gain rate and mean movement rate for manipulation of (a) mean territory quality (b) the amount of variation between territories and (c) the rate of turnover of territories. All model parameters not indicated are as given in Table 8.1. Note the increased scale for movement rate in comparison to figures 8.1 and 8.3.

Amount of variation in territory quality (σ): Fig. 8.2b

When the between-territory variance in quality is increased, the effect on the gain rate of individuals is dependent upon their competitive ability. Thus, as σ increases the best competitors do much better whilst the poor competitors do much worse than at lower values of σ . This is because as σ increases, the value of the best territories increases whilst the value of the worst territories decreases. Therefore, variance will be beneficial to good competitors as they will generally get the best territories whilst the poorer competitors which are relegated to the poorer territories obtain even less resources when they manage to obtain any at all. Again, because we change all patches equally, there is no substantial effect on movement patterns.

Rate of turnover of territories (C): Fig. 8.2c

Increasing the rate at which territories qualities change can be expected to have several effects. Individuals on good patches can exploit them for less time before perhaps having to move. At the same time, poor patches will increase in quality more frequently and so individuals “trapped” in these areas will be likely to benefit from an improved patch more often. However, the net result of these effects is that rate of turnover has very little effect on rate of resource gain across the range of ranks. Movement rates increase with rate of environmental change as one would expect.

Memory parameter (α): Fig. 8.3a

The rate of discounting of previous experience appears to have little effect on patterns of resource gain. Movement rates for any given rank are inversely related to α . However, the magnitude of this effect is small, and provided α is not extremely high (such that individuals have a very short memory, and are highly influenced by their current situation), we would not expect this parameter to affect model predictions. This is particularly the case as we ignore the initial part of a simulation, and consider only the “equilibrium” phase where the individuals have learnt about their environment and have relatively stable expectations.

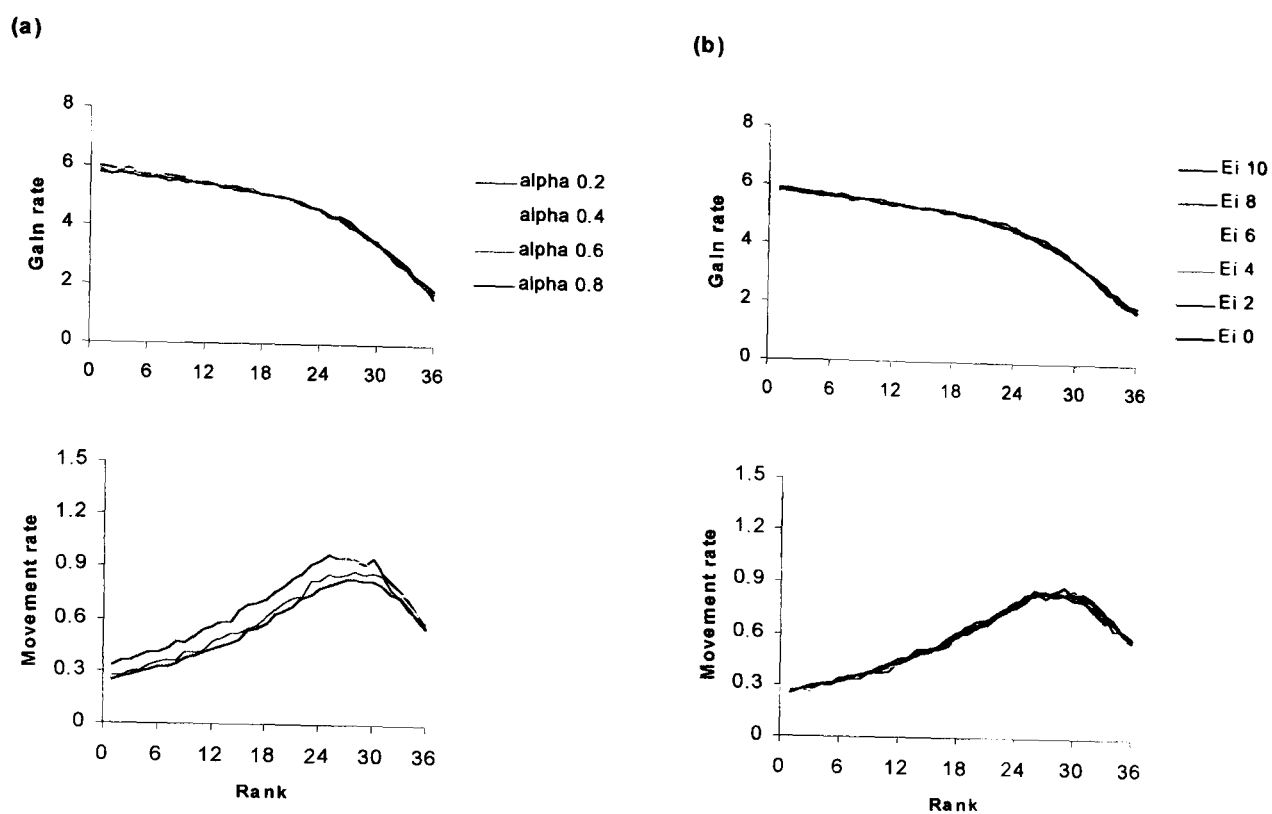


Figure 8.3. Plots of mean gain rate and mean movement rate for manipulation of (a) the memory parameter and (b) the initial patch estimate. All model parameters not indicated are as given in Table 8.1.

Initial patch estimation (E_i (initial)): Fig. 8.3b

As can be seen, the initial expectation values assigned to each individual have no significant effect on either long-term rates of gain or movement. As outlined previously, this is because the initial part of the simulation is ignored when calculating the model outputs.

Discussion

The model generates three main predictions. First, when the number of animals exceeds the number of patches, there is a sigmoidal relationship between dominance rank and resource gain. Secondly, middle-ranking animals are more mobile than those of high or low ranks. Thirdly, the geometry of relative patch orientations has a major effect on resource gain and movement patterns only when the array of patches decreases in one dimension to one patch wide. The numerical values of the variables in the model do not affect these basic model characteristics. The model is driven by three fundamental components. First, an animal moves, or attempts to move, when its rate of resource gain falls below the average it can remember having experienced. This is a simple derivative of learning theory (Bernstein *et al.* 1988 and references

therein). Secondly, an animal cannot move into space used by a more dominant individual. This assumption seems reasonable for very aggressive animals occupying areas of space that they can defend easily. Elaboration of the model would allow us to test the effect of relaxing the condition (i.e. reducing aggression either generally or between specific individuals). Thirdly, when subordinate animals are forced to share space with a dominant, they gain no resource. This component of the model is likely to vary depending on the detailed behaviour of different species of animal in different contexts. For example, the assumption might not apply when there is an opportunity for subordinate animals to hide and harvest some resource undetected by the dominant individual. However, such deviations from the basic model would be likely only to vary baseline resource intakes rates and not the general pattern of predictions. We expect the three key predictions above to be robust, and so generally observable in natural and laboratory systems. Although they can be understood in terms of the underlying model structure, they would not be predicted by the classical IDD model. Hence, they should form a useful basis for critical comparison between our model and the IDD.

We consider only a very simple set of rules for patch choice, namely that choices between available patches are random, and if there are no neighbouring patches which are unoccupied or occupied by a subordinate individual, then no patch change is made. However, there are other alternative rules that may be at least equally plausible. For instance, since dominant individuals tend to benefit from higher gain rates, in stable environments, a more effective rule could be to move into the patch containing the best of those individuals that are subordinate to the focal individual. Similarly, for animals on a territory held by a better competitor (floaters), alternative rules to staying put could be choose the neighbouring territory held by poorest individual, or even to choose the adjacent territory of the owner who does not have floaters dominant to the focal individual. Thus, these alternative rules could act as adaptations to variable environments where good competitors may well move on in response to decreases in gain that might be tolerated by a less successful individual who, if they used this tactic, could benefit from the better competitor's higher expectations. These alternatives are likely to produce some different results, but tend

towards becoming different strategies in the sense of more complex ESS games. Our aim was to produce a relatively simple and robust model: examination of other movement rules and their effect on the model predictions would, however, be a fruitful direction for future work.

In the basic model presented here, despite short-term spatial variation, the environment is homogeneous in the long term since each patch varies with the same distribution of values. This is not likely to be the case in many natural systems. Some areas are likely always to be better than others on average, and different distributions of resource availability may apply to different regions. There may also be temporal patterns in mean resource availability. For example, abundance of invertebrate drift in streams follows diel cycles (Allan 1995). Our model generates predicted patterns of movement and resource intake in the absence of complex, time-invariant or systematic, environmental variation, and so provides the default against which more complex systems may be compared.

The next stage in the development and application of the model will be to test it under suitable conditions of resource availability. Ideal test subjects are stream-dwelling salmonid fishes, which have been used extensively in studies of territoriality (e.g. Dill 1978, Grant & Kramer 1990). The structure of the model appears to be appropriate to this taxon. In laboratory studies, dominant fish aggressively defend favoured patches and track temporal variations in patch quality (Gotceitas & Godin 1992). In heavily populated habitats, subordinate fish may share patches with dominant individuals but exhibit low rates of food intake (JD Armstrong unpublished data.). In near-natural systems there is much variation in mobility of individual fish tracked using passive integrated transponder tags (Armstrong *et al.* 1996, 1997) with some salmon parr moving extensively between patches, which vary relative to one another in time and space (JWA Grant & JD Armstrong, unpublished data).

The value of developing models to relate resource intake to distributions of resources and foragers can be illustrated by considering growth patterns of Atlantic salmon parr. The sigmoidal relationship between resource intake and rank would generate a

bimodal distribution of growth rates within populations even if phenotypic characters, such as metabolic rate, did not vary between individuals. Such bimodality has been noted for tank-reared salmon (Thorpe 1977) and in the wild (Heggenes & Metcalfe 1991). The cause of bi-modality in tanks is thought to be innate variation in appetite (Thorpe *et al.* 1992). The output of our model raises the possibility that an interaction between environmental heterogeneity and a linear dominance rank may also produce bi-modality. Future work could usefully investigate the consequences of changes in resource production rate where changes are not random, but correlated in time and/or space.

One important feature of the model is that populations occupying linear arrays of single patches will differ distinctly from larger (and in many cases more natural) systems. Therefore, we recommend that arenas larger than one patch across are used for research into links between behaviour and population dynamics, if conclusions drawn from such systems are to be extrapolated to larger spatial scales. In addition, territories in the real world are unlikely to form a Cartesian grid (Hamilton 1971) and the number of neighbouring territories for any patch need not be constant. However, as mentioned previously, our aim was to present a relatively simple model as an alternative to the IDD which can be tested and then modified in the future. More realistic spatial representations of neighbourhood structures seems another fruitful line for such development.

Although our model is simple, it has generated interesting and important predictions. We have focused on variation in movement and resource intake as main response variables and have considered a habitat that is homogeneous in all respects except short-term temporal variation in the distribution of food resources. The model could be elaborated, in much the same way that the IFD has been developed, to incorporate variation in the environment, such as spatial and temporal variation in mortality agents, and responses of various components of fitness. While we suggest that salmonid fishes are a good test subject, we hope that the model will also be tested on other taxa to establish whether we have identified simple general structures underpinning the ecology of diverse systems.

Acknowledgements

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**ASSESSING THE ODDITY EFFECT: THE ROLE OF BODY SIZE AND
COMPETITION**

Introduction

Group living animals may gain foraging advantages, for example as a result of shared vigilance, when predator detection is shared between group members, allowing individuals to spend more time foraging (Pulliam & Caraco 1984). In addition, many other factors that decrease the predation risk of animals in groups have been proposed (see Pitcher & Parrish 1993). However, vulnerability to predation may not be the same for all members of a group, due to differences in individual traits. For example, individuals that are phenotypically different from the rest of the group may be conspicuous to visually hunting predators and suffer higher predation rates (Landeau & Terborgh 1986, Theodorakis 1989).

The idea that predation risks for such 'odd' individuals may be important in the formation of phenotypically uniform fish shoals has received much attention in recent years (e.g. Ranta *et al.* 1992, Krause *et al.* 1996, Peuhkuri *et al.* 1997). Much of this work suggests that size-assortative shoaling reduces phenotypic oddity within groups. For instance, both Krause (1994) and Peuhkuri (1997) showed that fish appear to make a trade-off between feeding and predation risk, and that this trade-off is linked both to their own phenotype and the frequency of different phenotypes (measured in terms of body size) within the shoal. In both studies, single large fish had lower feeding rates in shoals of smaller conspecifics than when in groups of uniformly large individuals.

Peuhkuri (1998) measured feeding rates of individuals in groups differing in their composition (the proportion of 'small' to 'large' fish in the group), in order to evaluate whether they adjust their perceived predation risk in relation to their relative 'oddity'. She demonstrated that the reduction in feeding rates of large threespine sticklebacks (*Gasterosteus aculeatus*) in shoals of small conspecifics varies in a frequency dependent manner, as would be expected if the oddity effect is responsible for this behaviour. However, small fish in a group of predominantly large fish responded differently from large fish in the converse situation: the feeding rate of small fish was unaffected by these changes in group composition. In summary Peuhkuri (1998) stated that "...these results imply that oddity has less to do with small individuals' tendency to avoid associating with larger conspecifics than some other factors may have". She further concluded, "... oddity does not seem to trouble small individuals" (p. 336).

This chapter examines what these “other factors” might be, and postulates an alternative to Peuhkuri’s conclusion that the lack of a response of small fish to oddity in her experiment indicates that small fish do not suffer from an oddity effect. More generally, the point is made that there is a danger, when looking for a response to an effect, that the apparent absence of a detectable response may be misinterpreted as an absence of the effect itself. In fact, the response may simply be suppressed due to an even greater but opposing pressure from another factor. The intention is not to criticise what is an elegant experiment, but rather to suggest alternative interpretations of results presented by Peuhkuri (1998).

Physiological differences

The following explanation can be proposed for differential responses of small and large fish to phenotypic oddity. Previous studies have shown that both small and large fish are subject to higher predation risks when odd in a shoal (Theodorakis 1989), and that both small and large fish have a preference for fish of similar body length (e.g. Ranta *et al.* 1992, Krause 1994). However, the behavioural response of small fish to the oddity effect is probably constrained by physiological factors that do not apply to large fish to the same degree. Studies have shown that larger fish have a greater mass-specific metabolic efficiency than small ones (e.g. Wootton 1994, Krause *et al.* 1998) and that the weight-specific energy cost of maintenance declines as the weight of the fish increases (e.g. Lester 1971, Meakins 1975, Brett & Groves 1979). Further, Wootton *et al.* (1980) provide data on the effect of temperature and body weight on routine metabolism for sticklebacks. This can be used to calculate metabolic expenditure per day per mg of fish weight for fish in the size range used by Peuhkuri (1998). Peuhkuri used two size classes of fish, ‘small’ (approximately 35mm long) and ‘large’ (approximately 60mm long), and her experiments were carried out at between 15 and 18°C. By referring to Wootton *et al.*’s (1980) figures, at 15°C a 0.4g fish (approximately 35mm long: Wootton 1976) has a routine metabolic rate of close to $0.138 \text{ Jmg}^{-1}\text{d}^{-1}$, whilst that of a 0.80g fish (approximately 50mm long, i.e. smaller than the 60mm fish used by Peuhkuri) is $0.089 \text{ Jmg}^{-1}\text{d}^{-1}$. At 17.5°C the comparable figures are 0.175 and $0.103 \text{ Jmg}^{-1}\text{d}^{-1}$ respectively. Therefore, the energy needs per unit weight of Peuhkuri’s large sticklebacks are between 35 and 41% lower than those of her small ones over the temperature range used in her experiments. This can be considered as a

conservative estimate as Peuhkuri's large fish were slightly larger than those used by Wootton *et al.* (1980). As a consequence of this higher weight-specific energy usage, small fish lose a larger proportion of their weight than large fish following food deprivation (Fig. 9.1). This almost certainly means that the costs in fitness terms of missed feeding opportunities are greater for small individuals compared to large ones.

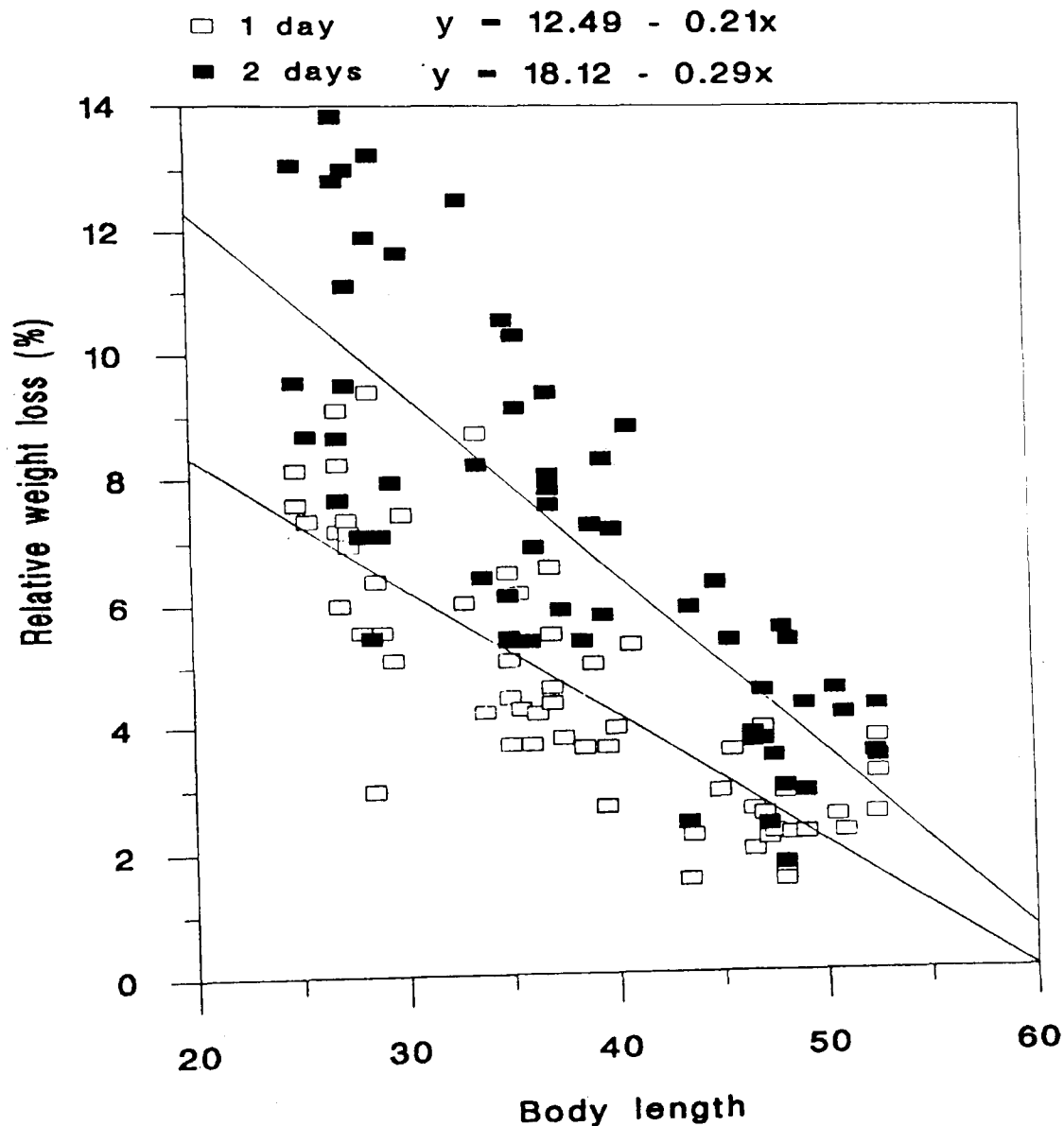


Figure 9.1. Relationship between body length (mm) and relative weight loss ((absolute weight loss / initial weight) \times 100) as a function of the duration of food deprivation in threespine sticklebacks: one day of deprivation, $N = 60$, $r^2 = 0.68$, $p < 0.001$; and two days, $N = 60$, $r^2 = 0.62$, $p < 0.001$. After Krause *et al.* 1998.

Applying the relationship described in Fig. 9.1 to fish of the size classes used in Peuhkuri's (1998) experiment, it can be seen that small sticklebacks (35mm) may expect to lose 5.1% body weight over the 24hr pre-trial starvation period, compared to a

loss of only 1.4% in large (53mm) fish. Again, the latter figure is a conservative estimate, suggesting an even lower percentage weight loss in Peuhkuri's large fish. The relative weight loss of small sticklebacks in her experiment is thus likely to be more than three times that of large fish. If so, it would be reasonable to expect the trade-off between foraging activity and predator avoidance to be shifted more towards foraging in small fish than in large ones. The absence of an apparent response to phenotypic oddity could therefore be caused by differences in metabolic expenditure between small and large fish.

When part of a shoal of non-matching fish, large fish apparently increase their vigilance rates at the expense of reduced feeding rates (Krause 1994, Peuhkuri 1997, 1998). Large fish are able to do this as the physiological costs of lost feeding opportunities are relatively low for them, because they have both lost less of their reserves and have a greater ability to obtain resources through their competitive advantage (Gill & Hart 1996). In contrast, small fish do not change their vigilance and feeding rates, perhaps because they cannot afford to miss out on available feeding opportunities. The argument here is not that these fish are oblivious to predation risk, rather that changes in time spent in vigilance with changes in predation risk will not necessarily be predicted if fish are prioritising food over predation risk. If food acquisition is important enough, then I suggest that the smaller fish will feed at a constant rate, limited by either their ability to gather resources (due to their lower competitive ability) or by a minimum threshold for time spent on vigilance. Thus, smaller individuals, under greater metabolic stress (or increased motivation to feed) than their larger conspecifics, may judge food acquisition to be more important than the risk of predation. It is known that hungry sticklebacks are willing to accept greater risks of predation in order to feed than those that have been recently fed (Fraser & Huntingford 1986), and so their need to forage more actively means that small fish may show very little variation in vigilance in response to different predation risks. Thus, the difference in behaviour between small and large fish may be caused by different metabolic constraints, rather than by differential effects of oddity on predation risk. Small fish do increase their preference for size-matching partners under certain conditions, notably when escaping from predators (as discussed by Peuhkuri (1998, p.336)).

Furthermore, even if the differences in weight loss seen in Fig. 9.1 were entirely due to differences in gastric evacuation times (since guts may be emptying during the initial period of food deprivation), then evacuation times are likely to be both shorter in small fish and equate to a larger amount of food in proportion to body weight. Rate of food intake and motivation to feed are known to be closely linked to both stomach fullness (Brett 1971) and rate of gut emptying (Godin 1981) in salmonids and it is unlikely that this will differ for sticklebacks. If motivation to feed is controlled by stomach fullness (Hart & Gill 1992) then these small fish will experience a longer period of increased motivation. Thus, if small fish empty their stomachs faster then they should be hungry earlier, and if they are starved for the same time as large fish then they will be hungrier for longer.

Consideration should also be given to additional factors which may make interpretation of Peuhkuri's experiments more complicated. Specifically, the fact that predation risk varies with body size (e.g. Ricker 1979 in Werner *et al.* 1983) may mean that small fish are more vulnerable to predation risk in general. Thus, small fish may also have a greater need for growth due to the long-term benefits of larger size (e.g. lower predation risk: Werner *et al.* 1983, increased fecundity: Bagenal 1978) that could increase their motivation to feed.

Competitive differences

Peuhkuri (1998) rejected the idea that competitive effects could provide a convincing explanation for observed changes in the foraging activity of larger individuals. Her argument rests on two assumptions. The first is that food presented in excess "should prevent direct competition for food items interfering with the possible effects of oddity on individual foraging activity" (p. 334). Secondly, although she acknowledged the argument that the increase in foraging activity by larger individuals with their frequency in the shoal might be explained by scramble competition even if food was not limiting (*sensu* Clark & Mangel 1986), she predicted that if competitive effects are present, the foraging activity of the larger fish would be expected to increase in proportion to their numbers in the shoal. The possibility that neither of these assumptions may hold in generality is discussed below.

It is quite possible that interference competition may still be occurring in the experimental situation described, despite the excess of food. Physical competition is not necessary for interference, in that the mere presence of potential competitors nearby may change the way in which an individual forages (Cresswell 1997 and references therein). The possibility of interference will be increased if experimental food is presented in a different way to their recent experience and so consequently individuals are unsure as to how much food will be available to them, and for how long. It is not implausible that this type of situation could have occurred in the experimental set-up described in Peuhkuri (1997, 1998). Thus, it could be argued that the increase in the proportion of large fish in the shoal could lead to decreases in their intake rate (intake per unit effort), which are to some extent compensated for by increases in foraging activity. When large fish are relatively uncommon in the group, their feeding activity may be lower than that of the smaller fish in the shoal (because of the greater feeding efficiency of larger fish), but may become elevated as the frequency of larger individuals increases (as appears to be the case in Peuhkuri's experiments). In contrast, the smaller fish in the shoal will continue to forage at a constant rate, as discussed above. As the frequency of larger fish in the group increases, physical limits to their foraging rate (e.g. the finite time required to handle captured food items) are likely to come into effect. This means that foraging activity cannot continue to increase in proportion to the number of large individuals in the shoal, even without the problems of increasing interference. Thus, competitive effects may not necessarily result in proportional increases in foraging activity with an increased frequency of large individuals.

Finally, the question of feeding efficiency would appear to be quite important in this situation, but the observations made by Peuhkuri (1998) do not allow the determination of changes in this parameter. As Peuhkuri (1997, 1998) states, measurements of time spent foraging and number of strikes are not a direct measure of intake, as the 'strike efficiency' remains unknown. It is quite possible that the increase in the number of strikes made by large fish seen in Peuhkuri's experiment may be due to increased interference as the number of large fish in the group increases. Increased competition for food may lead to an increase in both the amount of time spent foraging and the individual's strike rate. A plausible reason for the systematic variation in success per strike required for this argument may itself be an effect of interference competition:

increased anti-predator vigilance results in reduced accuracy of discrimination of food items (Metcalf *et al.* 1987) and such discrimination could just as easily be affected by an increase in interference from other individuals.

These arguments are presented as equally likely scenarios that should not be excluded without firm empirical evidence. By the same token, it is important to re-emphasise that the interpretations of Peuhkuri (1998) cannot be refuted, but should not be considered any more plausible than the alternatives proposed here. This discussion underlines the importance of addressing size constraints when experimental trials seek to compare the behaviour of fish of different sizes. Familiar techniques such as using food deprivation to standardise hunger levels are likely to affect small and large fish to different degrees. Differential periods of food deprivation calculated to produce effects of similar magnitude (for example, 2% reduction in body weight) may be one way of tackling this problem. In conclusion, other factors, such as differential metabolic expenditure and competition, must be taken into account when assessments of the effects of oddity are made.

The future

Although differential periods of food deprivation may offer one way of resolving the problems associated with size-specific metabolic efficiency, the technique is likely to be difficult to implement. In addition, it only addresses one of several issues, and another approach is needed to enable us to tease apart the importance of the various effects discussed above. The complexity of the situation is such that verbal arguments are unlikely to be able to fully explain the observations that have been made, as there are a number of potential mechanisms that act in conflicting directions. This leads one to the conclusion that the only way to resolve this question is to look at the magnitude of the various effects in relation to predictions from optimality models carefully parameterised for sticklebacks. Development of an individual-based model would allow the elucidation of the importance of various mechanisms influencing the results found by Peuhkuri (1998). Such a model would lead to a set of clear predictions that could then be tested empirically. The following paragraphs set out a general framework on which this model could be based.

An individual-based model in which individuals are summarised by their phenotype seems the best starting point. The basic problem can be addressed by designating only two phenotypes: 'large' and 'small'. The proportions of each of these phenotypes will be varied so that the compositional changes characteristic of Peuhkuri's experiments can be emulated. An individual's phenotype will determine its competitive ability, food requirements and susceptibility to interference. For instance, a simple function could be used to describe an individual's motivation (or need) to feed in relation to the amount of time it has been deprived of food, which could also differ according to phenotype. This function could easily be determined for sticklebacks from a combination of data from the literature and experimental calibration. Similar functions could be used for the relationship between phenotype, oddity and predation risk, or phenotype, oddity and the strength of interference. Obviously not all such parameters could be determined empirically, but parameterising the model for real fish as far as possible should be a priority.

Simulations will consist of allowing individuals to find their optimal feeding rates (i.e. that which balances feeding requirements with perceived predation risk), in shoals of varying composition. Variation of the functions which describe an individual's risk, activity and motivation will allow the model to be finely adjusted until its predictions for foraging effort match those found by Peuhkuri (1998). It will then be possible to determine which of the phenotypic differences (oddity effect, interference or food requirements) provides the most likely explanation for Peuhkuri's results. Further elaboration of the model could involve exploration of other size-related factors that may affect the behaviour of individuals in shoals of mixed sized fish. Specifically, size-related predation risk and the need for growth in the light of the long-term benefits of size. The predictions produced by the model will be testable and subsequent analysis will also allow exploration of the circumstances where these different mechanisms for the pattern of feeding rate change make different predictions. Such circumstances might include the effect of increasing predation risk on a shoal of fixed composition, increasing the difference in food requirements between phenotypes, or differentially varying the oddity effect for the two phenotypes. These different predictions, if found, should lead to the design and execution of further experiments which will critically test for the

mechanism(s) underlying Peuhkuri's results.

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GENERAL DISCUSSION

Summary

Although IFD theory is branching out into a number of different areas, it is still a cohesive framework against which we can consider animal distributions. This cohesiveness is provided mainly by the strong link between theory and empirical approaches that has characterised studies of the IFD and set them slightly apart from the majority of other ideas in behavioural ecology. This thesis upholds this tradition by using both experimental and theoretical analyses to address model assumptions.

IFD theory in practice

Since its inception, IFD theory has been shown to be incredibly robust to violations of some of its most basic assumptions. Indeed, it has been considered by many to be one of the most successful predictors of animal distributions to date (Talbot & Kramer 1986, Milinski 1988, Milinski & Parker 1991, Tregenza 1995, Sutherland 1996). The main strength of the theory, its broadness, is best explained by Milinski and Parker (1991, page 142) when they state that “at its most general level we can use ideal free theory to make predictions about any strategic choice in which the fitness consequences of adopting a particular strategy decline with the number of other individuals exploiting the same strategy.” As an example, Sibly’s (1983) discussion on the concept of optimal group size uses ideal free theory to show that optimising animals may, through incomplete knowledge and timing, actually form groups of greater than optimal size. Other examples of IFD theory used in a novel way include its use in understanding the timing of ontogeny and mechanisms of niche separation (see Sutherland 1996 and references therein).

However, the fact that IFD theory can be applied to a wide range of seemingly different situations does not guarantee its eventual use as a generalised model of animal distributions. Indeed, instead of producing an increasingly realistic single model of heightening complexity, the development of ideal free theory has led to a large number of models, each of which addresses one or two of the major assumptions of the theory separately (Tregenza 1995). While IFD theory is unusual in that it consistently shows strong links between theoretical work and empirical tests, theorists are now inclined to argue about a smaller and smaller subset of models which may not address a wide range of biological situations (e.g. Doncaster

1999, Rita & Ranta 1999, Sutherland & Parker 1999). Increasingly, IFD models are also tailored to deal with one or two specific cases. This, along with recent observations on the sensitivity of many IFD-related models to initial conditions and small perturbations in parameters or movement rules (e.g. Houston & Lang 1998, Hugie & Grand 1998, and chapters seven and eight of this thesis), suggests that a single unifying theory of animal distributions is unlikely to appear. Although the current exponential expansion of microcomputer capacity has helped ecologists greatly, it is highly unlikely that any model will be able to produce specific predictions for a wide range of complex systems. Mangel and Clark (1988, paraphrasing Oster and Wilson 1978), provide a good example of the problems currently facing those modelling biological systems. They point out that “any behavioral model which is simple enough to be operational is necessarily too simple to be biologically realistic. Obversely, any biologically realistic model in behavioral ecology will be too complex to be operational (and, we might add, to be mathematically tractable).” As chapter three illustrates, for some cases at least, it appears likely that there may not be any general rules for the dynamics of complex interactions between individuals. Although accurate predictions can be made, they require very specific information from the system under study, and differences between systems mean that predictions are not applicable to a single generalised case. This result may be disturbing to some, but its implications are clear. Despite the advantage of its aforementioned robustness, a single IFD model is unlikely to be able to deal with the complexity of producing truly generalised predictions of animal distributions whilst remaining simple enough for general use.

Despite this rather sombre suggestion, it should be remembered that IFD theory is still an effective tool for predicting animal distributions with reasonable accuracy in a wide range of situations. Ideal free theory will clearly benefit from more empirical and theoretical work addressing the question of inappropriate assumptions. It is important that ‘hidden’ assumptions, built into the modelling methods themselves, should also be considered in this way. For instance, the infinitely large populations assumed in many analytical studies of IFD theory are not likely to be well approximated in nature. The use of such large population numbers allows the stochastic nature of individual movements to be ignored (Wilson 1998). However, in

the situations commonly examined as tests of IFD theory, where relatively few individuals are involved, such stochasticity is an integral part of the system, both in terms of individual movement and for resource acquisition, a fact currently considered by only a few workers (e.g. Houston & Lang 1998, Rita & Ranta 1998a, b, and chapter seven of this thesis). Thus, predictions from such analytical models may not be strictly applicable to experimental tests and field observations where the number of individuals considered is frequently much less than 100 (Hugie & Grand 1998, and see chapter seven of this thesis). Although the importance of such rigorous mathematical analyses (and their implicit assumptions of infinite populations) to IFD theory is clear, and their development essential to our understanding of the subject, the value of individual-based models with realistic numbers of individuals to compare results with empirical work should not be underestimated. Such 'intermediate' models should be used more often as an effective and necessary bridge between empirical studies and pure analytical theory.

The future of IFD theory

One of the next progressions for IFD theory will be the obvious, and often called for, thorough empirical examination of interference. Studies of this type are currently being spearheaded by Goss-Custard and others (Goss-Custard 1980, Ens & Goss-Custard 1984, Stillman *et al.* 1996, Norris & Johnstone 1998, Triplet *et al.* 1999) and Cresswell (1997, 1998), working with oystercatchers and blackbirds (*Turdus merula*) respectively. A clear understanding of both the mechanisms behind interference and the way in which interference affects individuals in differing situations are urgently needed if interference IFD models are to progress. Examination of the consequences of differential effects of interference between patches on predicted distributions (chapter five) indicates that previous empirical results may be explained by this conceptually simple, but theoretically unexplored idea. Thus, the lack of true truncation of individuals in practice may be due to a recognised, but overlooked factor.

A second goal for those working on IFDs should be the recognition that many of the animals used in tests of IFD theory form relatively cohesive *social* groups. Therefore, these animals are likely to interact and pass information in ways unrelated

to the resource being considered by those studying them. Some of these 'non-IFD factors' have been recognised (e.g. Abrahams 1989, Hugie & Grand 1998), and one in particular, predation risk, has been examined in great detail from a variety of perspectives (e.g. Utne *et al.* 1993, Utne & Aksnes 1994, Moody *et al.* 1996, Grand & Dill 1997, Peuhkuri 1997, Peuhkuri *et al.* 1997, Utne & Bacchi 1997, Utne *et al.* 1997, Peuhkuri 1998). However, it is only recently that some of these factors have begun to be examined in the context of IFD theory. Incorporation of variation in traits other than those related to competitive ability has also been neglected. These post-acquisitional phenotypic differences are widely recognised in the literature and should help both to draw IFD theory into more fields, and to expand our knowledge of how individual differences can influence animal distributions. Examples of this approach include a novel treatment of the IFD by Focardi S., Farnsworth K.D., Poli B.M., Ponzetta M.P. & Tinelli A. (in submission), and chapter six of this thesis. The former example explores the idea that sexual segregation of ungulates (in this case fallow deer, *Dama dama*) may be driven by sexual size dimorphism in the context of scramble competition.

The use of information within socially foraging groups is also a pertinent area of research that addresses the assumption of perfect knowledge on the part of foraging individuals. Animals are known to be capable of learning about patch profitability from others, an area of research currently being pursued by a number of groups (e.g. Templeton & Giraldeau 1996, Beauchamp *et al.* 1997, Rita & Ranta 1998a, c, Smith *et al.* 1999, and Giraldeau 1997 for a review).

Finally, the questions discussed in chapter nine of this thesis, namely predation risk and phenotypic differences in physiological parameters, touch on the importance of 'state' in studies of individual decision-making. State-dependent IFDs (McNamara & Houston 1990) have been championed as the future of IFD theory (e.g. Milinski & Parker 1991, Tregenza 1995), because of their ability to provide a common currency for a number of different trade-offs an animal may make. Unfortunately, progress in this area has tended to remain in the realms of theory, with few empirical tests (e.g. McNamara & Houston 1990, Burrows 1994, Giske *et al.* 1997). However, consideration of size assortative shoaling in fish (Ranta & Lindstrom 1990, Ranta *et*

al. 1992, Peuhkuri *et al.* 1997, Peuhkuri 1997, 1998, and chapter nine) would appear to be a worthwhile candidate for this type of modelling. Development and testing of state-dependent models will undoubtedly form a major part of work on IFD theory in the future.

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