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The relationship between continuous input and interference models of ideal free distributions with unequal competitors

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Abstract. Fretwell's (1972, *Populations in a Seasonal Environment*, Princeton University Press) ideal free model predicts the ideal distribution when individuals in a habitat are free to move between patches. In this paper, the relationship between the 'continuous input' and 'interference' ideal free models of Sutherland & Parker (1985, In: *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*, ed. by R. M. Sibly & R. H. Smith, pp. 255–274, Blackwell) and Parker & Sutherland (1986, *Anim. Behav.*, **34**, 1222–1242) are examined. Continuous input describes cases where resource items arrive at patches containing groups of waiting competitors. Increasing their density in a patch reduces individual gain rates because the resource items arrive at a fixed rate, and are shared between competitors. Interference describes cases where foragers search for prey items hidden within the patches. Increasing competitor density in a patch can reduce individual gain rates due to interference between individuals. Both can be modelled using the form: individual gain rate $= Q_i n_i^{-m}$, in which Q_i is the input rate or prey density in patch i, n_i is the number of competitors, and m is a constant which increases with the strength of interference. A previous formulation of the above model in which individuals have unequal competitive abilities is extended to cover the case where phenotypic differences are reflected by a scaling of Q_i (rather than by a scaling of the level of m). Here, many different mixed distributions of phenotypes can exist as ideal free equilibria, provided that relative competitive abilities stay constant across patches. Many different phenotypes can occur across several patch types. However, where phenotypic differences are best reflected by a scaling of m, then these mixed distributions of phenotypes are not possible, and no more than one phenotype can play a mixed strategy across the same pair of patch types. Typically, a truncated distribution of phenotypes between the patches can be expected, with the best phenotypes in the best patches. Some general conditions are proposed for ideal free distributions of unequal competitors.

Fretwell's (1972) familiar ideal free model predicts the ideal animal distribution when individuals in a habitat are free to move between patches. Recent studies of the ideal free distribution have drawn a distinction between two types of resource use (Sutherland & Parker 1985; Parker & Sutherland 1986; Milinski & Parker 1991). In one, termed 'continuous input', the competitors scramble for as large a share of the incoming resources as possible. This might apply, say, to fish competing for arriving food (e.g. Milinski 1979), or to males competing for arriving females (e.g. Parker 1970). Resource items arrive at patch i at a given rate Q_i to the group of n_i competitors in i. Eating or mating takes place on arrival, and the expected gain rate to each competitor is thus Q_i/n_i.

In contrast, in the 'interference' model of resource use, the amount of resource stays approximately constant in the short term but the presence of others reduces the gain rate due to interference effects, e.g. fighting or disrupting prey (Goss-Custard 1980). This situation is probably the norm for many foraging vertebrates and some invertebrates. The density of prey items stays roughly constant because depletion is insignificant over a short period. The instantaneous gain rate would therefore be constant as Q_i and independent of the number of competitors n_i, were it not for the effect of interference. One of us (Sutherland 1983, following Hassell & Varley 1969) has suggested that the gain rate to each competitor could be described by Q_i/n_i^m, where m increases with the strength of

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interference. Since zero interference must yield a gain rate of Q_i, the range for m must hence be $0 \leqslant m \leqslant \infty$.

GENERAL MODEL

Though not stated explicitly in Sutherland & Parker (1985) and Parker & Sutherland (1986), effects that are mathematically similar to interference may occur in cases of continuous input. If, for example, some of the resouce items are destroyed in the scramble between competitors, then Q_i/n_i is no longer a proper description of gain rates. This resource wastage is likely to be an increasing function of the number of competitors in the scramble, so that Q_i/n_i^m again can be used as a formal model. However, since zero wastage must here yield a gain rate of Q_i/n_i, the range for m must hence be $1 \leqslant m \leqslant \infty$. Note that resource wastage is not biologically equivalent to interference, i.e. time wasted in fighting or other interactions between competitors, for the following reason. With continuous input, random time waste due to interactions between individuals does not affect mean uptake rate. The total uptake of resources must equal the total input, hence if certain competitors are interacting, the resource items are allocated among the rest.

For an ideal free solution to apply, individuals move to patches in which their intake would be higher, until no individual can profit by moving. The distribution of equal competitors throughout the set of exploitable patches in the habitat (certain patches may not be worth using by even a single competitor) should stabilize so that the payoff or gain rate is the same in all exploitable patches. For continuous input, at equilibrium an individual's gain rate in patch i is

$$W_i(n_i) = Q_i/n_i^{-m} = c\,(\text{constant}), \quad \text{for } 1 \leqslant m \leqslant \infty \quad (1a)$$

and for interference

$$W_i(n_i) = Q_i/n_i^{-m} = c\,(\text{constant}), \quad \text{for } 0 \leqslant m \leqslant \infty \quad (1b)$$

Thus although the two cases are very different biologically, we nevertheless have an almost exact mathematical equivalence for the two models. The difference between them concerns only the range that m can occupy. Typically, most empirical studies of interference give values for m in the range $0 < m < 1$, and generally much below 1 (Hassell 1978). We know of no cases where resource wastage has been measured explicitly. In dung flies, some of the females arriving at the group of waiting males may be killed as a result of male–male competition (Hammer 1941). In general we expect wastage to be low, so that m lies just above, or equal to 1·0. Thus m appears unlikely to overlap for the two models, being much lower for interference than for continuous input.

This leads to the two principal results. First (all other things being equal) the set of exploitable patches would be a much smaller proportion of the entire set for interference than for continuous input. This arises as follows. If m is zero, it pays all individuals to be in the best patch. The adverse effects of competition become stronger as m increases (individual gain rates are depressed more by increases in n if m is high), and so the population becomes more spread out into the less profitable patches, and less dense in the profitable patches. Since continuous input has typically higher m, it should result in a greater use of the available habitat (more poor patches included), and lower competitor densities in the profitable patches, than interference.

Second, this idea can be used to predict the density-dependent nature of prey loss (see also Sutherland 1983; Lessells 1985). Assume that there is little or no prey wastage (or that wastage does not involve prey mortality). With the ideal free distribution, all predators will catch prey at the same rate, so that prey mortality will depend entirely on the distribution of predators. If $m < 1{\cdot}0$, the aggregation of predators results in a higher ratio of predators:prey in the sites of highest prey density, and thus produces spatial density dependence of prey mortality. If $m = 1{\cdot}0$, there is a constant ratio of predators:prey, and thus prey mortality is density independent. If $m > 1{\cdot}0$, there will be a lower predator:prey ratio in site of high prey density, and thus the mortality will be inversely density dependent. Density dependence is thus expected for interference studies and density independence or even inverse density dependence expected for continuous input.

It is, however, clear that there are often considerable differences between individuals in competitive ability which can affect the distribution of competitors (Monaghan 1980; Goss-Custard et al. 1982, 1984). The remainder of this paper is devoted to the case of unequal competitors.

SUMMARY OF TERMS

The patch types in a given habitat are i, j, etc.
Resource input rate to, or alternatively the intake rate in the absence of competition in, patch i is Q_i.
The phenotypes are A, B, etc.
The numbers of competitors in each patch are n_i, n_j, etc.
The 'competitive weights' (measures of competitive ability) of each A, B, etc. in patch i are K_{Ai}, K_{Bi}, etc.
The mean competitive weight of competitors in patch i is K_i.
Payoffs (W) are a function of an individual's competitive weight relative to the mean competitive weight for the patch, and also of the total number of competitors (of all phenotypes) in that patch.
The payoff of an A phenotype in patch i is thus $W_{Ai}(K_{Ai}, K_i, n_i)$.
A strategy is a choice of patch to search in; it may be conditional on an individual's phenotype: e.g. 'if A, search in patches type i and j; if B, search in patch k; etc.'

UNEQUAL COMPETITORS: EXPLICIT MODELS

We (Sutherland & Parker 1985; Parker & Sutherland 1986) used the explicit form in (1a) and (1b) above as a basis for models of ideal free systems where individuals are unequal in competitive ability. The payoff or uptake rate of a given individual of phenotype A in patch i was related to its competitive weight, K_{Ai}, relative to the mean competitive weight in patch i, K_i.

Continuous input was investigated by assuming that the payoff of this individual would be

$$W_{Ai} = (K_{Ai}/K_i)Q_i n_i^{-m} \qquad (2a)$$

where $m = 1$ (resource wastage was not modelled; see equation 1a). Interference was analysed by scaling m in equation (1b) by $(K_{Ai}/K_i)^{-1}$. This inversion ensured that the same hierarchical structure of phenotypes was preserved for both models (i.e. the phenotype with the highest competitive weight has the highest gain rate). Thus

$$W_{Ai} = Q_i n_i^{-m(K_i/K_{Ai})} \qquad (2b)$$

(see Parker & Sutherland 1986). Allowing for the inclusion of wastage in continuous input (equation 1a), it is clear that the main difference between these two modelling approaches is that in the first (continuous input), differences in competitive weight scale the effect Q_i; in the second (interference), differences in competitive weight scale the effect m.

We now appreciate that this choice of mode of action of phenotype is arbitrary, and a priori is not fundamentally related to the biological situation (continuous input or interference). The biological situation will exert a fundamental influence on the range and level of m, as explained above.

Taking logarithms, we can express equations (2a) and (2b) as

$$\log W_{Ai} = \log(K_{Ai}/K_i) + \log Q_i - m\log n_i \qquad (3a)$$

$$\log W_{Ai} = \log Q_i - m(K_i/K_{Ai})\log n_i \qquad (3b)$$

In reality, the average competitive weight, K_i, may change with the number of competitors, n_i. However, if we assume for heuristic purposes that K_i remains constant with n_i, the difference between (3a) and (3b) can be shown by plotting log payoff ($\log W_{Ai}$) against log competitor density ($\log n_i$). The intercept (but not the slope) will be influenced by phenotype in model (3a), whereas the slope (but not the intercept) will be influenced by phenotype in model (3b); see Fig. 1a, b. We show below that if phenotype affects only the intercept, the ideal free solution can be radically different from the case where phenotype affects only slope. First, we examine some of the general properties of an ideal free evolutionarily stable strategy (ESS; see Maynard Smith 1982) with unequal competitors.

TYPES OF DISTRIBUTION

In a habitat with several patch types and many competitors consisting of several different phenotypes, there are clearly vast numbers of permutations of possible distributions. We define a strategy as a choice of patch in which to search or wait for resource items; strategies may be pure or mixed. Thus individuals of phenotype A may play a pure strategy, e.g. 'exploit only patch i', or a mixed strategy, e.g. 'exploit patch i with probability p_{Ai}; exploit patch j with probability p_{Aj}, etc.'

Ideally, we seek for distributions that are ESS (Maynard Smith 1982) distributions. An ESS can be a set of strategies, one for each phenotype, such that no individual of any phenotype can profit by playing an alternative strategy. For instance, suppose at the ESS individuals of each phenotype play different pure strategies: each phenotype will be restricted to a particular patch type. When a

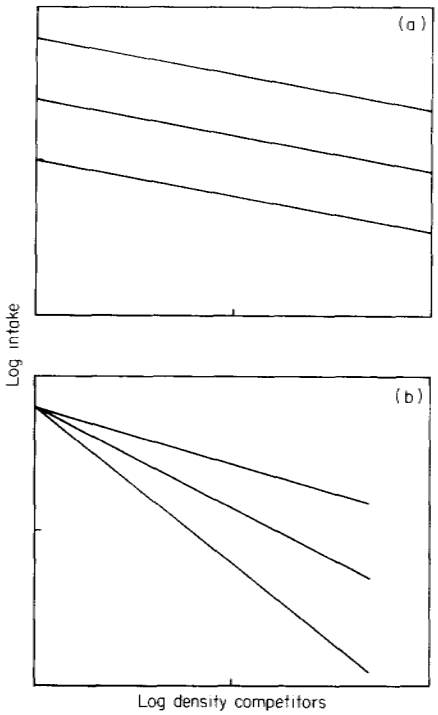


Figure 1. Relationship between payoffs of individuals differing in competitive weight, and the number of competitors in a patch, assuming that the average competitive weight remains constant. (a) Case where phenotype affects intercept, as modelled in equations (2a) and (3a). (b) Case where phenotype affects slope, as modelled in equations (2b) and (3b).

given individual deviates by entering the 'wrong' patch, it must achieve a lower payoff when all others play the ESS. But suppose that the ESS consists of some phenotypes playing mixed strategies (they are present in more than one patch type). Rare unilateral deviations in the strategy of individuals of these phenotypes are likely to give the same payoff as the ESS. We therefore require that these deviations, as they become commoner, must receive lower payoffs than non-deviating individuals of the same phenotype. This verbal description corresponds to Maynard Smith's two ESS conditions (see Maynard Smith 1982; Hammerstein 1984; Parker & Hammerstein 1985), as it relates to the case of phenotype limited strategies (Parker 1982; for formal definition, see Parker 1984). However, some of the subsequent analyses relate to distributions that are neutrally stable equilibria in the sense that they are attractors and, once attained, they will not shift by the action of natural selection (or differential reinforcement in the case of learning). However, there can be a set or continuum of such equilibria, such that if displaced (even locally, e.g. by drift) from one point, they may return to a different point.

For the present paper, we are concerned with two types of distribution, one is an ESS and the other a neutrally stable equilibrium.

ESS Truncated Phenotype Distribution

Suppose that a population of competitors consists of a set of discrete phenotypes, A, B, C, ... ranked in order of increasing competitive ability, so that A has the lowest competitive ability, and B the next lowest, and so on. This is the rank of phenotypes. They exist in a habitat in which the patch qualities increase in the order i, j, k, ... etc. This is the rank of patch qualities. In the truncated phenotype distribution, the rank of phenotypes is divided (truncated) between the rank of patch types, so that only individuals with adjacent competitive abilities may coexist in the same patch type. We (Parker & Sutherland 1986) called this type of solution the 'truncated phenotype distribution', and defined conditions for it to be an ESS. It is characterized by the fact that mixed strategies are restricted: no more than one phenotype can play a mixed strategy across the same two adjacent patch types in the rank order of patch qualities. Only the best and the worst phenotypes in a patch may be found mixing across adjacent patch types: the best may mix across into the next higher patch type, and the worst may mix across into the next lower patch type. The same rule applies if competitive ability is continuous, rather than discrete. The phenotypes that may show a mixed strategy are termed the 'boundary phenotypes'. Competitors with the highest competitive ability are found in the best patches, the next best competitors in the next best patches, and so on, with the worst competitors in the worst quality patches.

If the number of phenotypes is much greater than the number of patch types, most phenotypes play pure strategies (i.e. are found in only one type of patch), and several phenotypes play the same pure strategy, coexisting in the same patch. Typically, boundary phenotypes occur (and always occur if the phenotype distribution is continuous).

This solution was found both in interference models, and with continuous input if relative competitive abilities changed across patches. As an

example, suppose that patches increase in quality as i, j, k; and that phenotypes increase in competitive ability as A, B, C, ... J. The most competitive phenotypes (say H, I, J) occur only in the best patch (k), (say) E and F occur only in j, and the least competitive phenotypes (say A, B, C) occur only in the worst patch (i). D mixes between i and j, and G mixes between j and k.

Neutrally Stable Equilibria

Here, the general solution is that some or all phenotypes may be found playing a mixed strategy in the same two or more patch types. We found this form of distribution in our models of continuous input, when competitive ability stayed constant across patches. For large populations, such cases appeared to permit a continuum of equilibrium distributions. None is an ESS; the equilibrium attained depends on the starting condition.

We certainly do not claim that these two solutions (the ESS and neutrally stable equilibrium) are the only ones that can occur for ideal free distributions of unequal competitors. For example, with certain types of competition, it appears that there is neither an ESS nor an equilibrium distribution, and there can be cycling of competitors between patches (see Pulliam & Caraco 1984; Parker & Sutherland 1986; Schwinning & Rosenzweig 1990). Changing the mechanism of competition can, however, alter solutions of the equilibrium type to a unique ESS solution in which the distribution in each patch is the same as the summed distribution for the entire habitat (Korona 1989). However, they are the only types of distribution that we have been able to generate by the explicit models of unequal competition used in equations (2a) and (2b).

EQUILIBRIUM CONDITIONS

The following conditions do not differentiate between a unique ESS distribution (as in the truncated phenotype distribution) and a continuum of neutrally stable equilibrium distributions (as found in our previous papers for continuous input).

For a Given Phenotype to Play a Pure Strategy

Call ¥ an equilibrium distribution. For the A phenotype to play a pure strategy i, we require that all A individuals achieve a higher payoff in i than any individual A which switches to any alternative patch j, given that the distribution is ¥ and no other individual switches simultaneously. Hence

$$W_{Ai}(K_{Ai},K_i,n_i,¥) > W_{Aj}(K_{Aj},K_j,n_j,¥_{Aij}), \text{ for all j} \quad (4)$$

where $¥_{Aij}$ represents the equilibrium distribution altered only by the switching of one A from i to any alternative patch j.

For a Given Phenotype to Play a Mixed Strategy

For a given phenotype A to be present in more than one patch type, its payoffs must be equal wherever found; otherwise some A should move to the patch offering the highest reward. Thus for the A phenotype to play the mixed strategy of exploiting patches i, j, ... we need

$$W_{Ai}(K_{Ai},K_i,n_i,¥) = W_{Aj}(K_{Aj},K_j,n_j,¥) = \text{constant}, W_A \quad (5a)$$

where i, j, ... represent all patch types in which A is found. Unilateral deviations from the mixed strategy ($p_{Ai}^*, p_{Aj}^*, \ldots$) played by A will be penalized if

$$W_A > W_{Aj}(K_{Aj},K_j,n_j,¥_{Aij}), \text{ for all j} \quad (5b)$$

where $¥_{Aij}$ represents the equilibrium distribution altered only by the switching of a sufficiently small number of A from a given patch i to any alternative patch j. Condition (5b), if satisfied for all A playing a mixed strategy, ensures that ¥ is an attractor, but does not ensure that ¥ will be restored if multilateral deviations are possible. With the continuous equilibria found in our previous papers (Sutherland & Parker 1985; Parker & Sutherland 1986), it is clear that ¥ need not be restored after a unilateral deviation, since many phenotypes may profit by adjusting their strategies after a unilateral deviation.

If at the equilibrium a given phenotype (A) mixes across patches i, j, ... but avoids q, r, ... we also need a condition parallel to (4) to keep A out of q, r, ...

$$W_A > W_{Ar}(K_{Ar},K_r,n_r,¥_{Ar}), \text{ for all r outside i, j, ...} \quad (5c)$$

in which W_{Ar} is the payoff of an A switching to any patch r in which A is not represented at the ESS ($p_{Ar}^* = 0$).

RATIOS OF PAYOFFS IN THE TWO EXPLICIT MODELS

Our previous papers (Sutherland & Parker 1985; Parker & Sutherland 1986) suggested that the

truncated phenotype ESS distribution could occur in the continuous input model only when relative competitive weights differ for the various patch types. In the continuous input model, relative payoffs are proportional to relative competitive weights, but it is strictly the ratio of payoffs that is important.

We can differentiate between the two types of distribution by using a combination of the above conditions. For the truncated phenotype distribution, only one phenotype can mix strategies across a given pair of patch types. Consider patches i and j. Then if phenotype A is the boundary phenotype that mixes across i and j, from (5a)

$$W_{Ai} = W_{Aj}$$

Any other phenotype (B) that occurs in i must do worse in j, hence from (4)

$$W_{Bi} > W_{Bj}$$

Hence the ratio of payoffs of the two phenotypes in i cannot equal the ratio of payoffs of the two phenotypes in j

$$W_{Ai}/W_{Bi} \neq W_{Aj}/W_{Bj} \quad (6)$$

and so unequal ratios of payoffs across patches (6) is a necessary (but not sufficient) condition for a truncated phenotype distribution.

In contrast, if the truncated phenotype distribution does not apply, at equilibrium it can be possible for more than one phenotype to mix across the same two patches, and hence it can be possible for $W_{Ai} = W_{Aj}$ and $W_{Bi} = W_{Bj}$ simultaneously. Thus the ratio of payoffs of the two phenotypes in i can now equal the ratio in j (i.e. $W_{Ai}/W_{Bi} = W_{Aj}/W_{Bj}$).

Thus, if ratios of payoffs of more than one phenotype can be equal across the same two patches, we can rule out the truncated phenotype distribution; if ratios are unequal, the truncated phenotype distribution is a candidate solution.

Model 1: Phenotype Alters Intercepts

Suppose that the effect of phenotype is felt as in the continuous input equation (2a). Phenotype scales the intercept of equation (3a).

From (2a)

$$W_{Ai}/W_{Bi} = [(K_{Ai}/K_i)Q_i n_i^{-m}]/[(K_{Bi}/K_i)Q_i n_i^{-m}] = (K_{Ai}/K_{Bi})$$

Similarly, the ratio of payoffs in patch j for the same two phenotypes is

$$W_{Aj}/W_{Bj} = (K_{Aj}/K_{Bj})$$

If relative competitive weights remain constant across patches ($K_{Ai}/K_{Bi} = K_{Aj}/K_{Bj}$), then whatever n_i, n_j, Q_i, Q_j, or m, the payoff ratios will be equal.

Further, if relative competitive weights remain constant across patches ($K_{Ai} = K_{Aj}$ for all A), from (5a) it can be seen that any distribution of phenotypes that satisfies the relationship

$$(Q_i/K_i n_i^m) = (Q_j/K_i n_j^m) = \ldots \text{etc.} = \text{constant} \quad (7)$$

will be an equilibrium distribution. If $m = 1$, rule (7) says that, at equilibrium, the total competitive weight in a patch ($K_i n_i$) must balance the input rate (Q_i) in all patches (see Parker & Sutherland 1986). If $m \neq 1$, the input rate must be balanced by $K_i n_i^m$ for all patches.

However, if relative competitive weights change across patches, it is clear that only one phenotype can show a mixed strategy across the same two patch types, and (as we found) the truncated phenotype ESS is hence possible.

Model 2: Phenotype Alters Slopes

If the effect of phenotype is modelled as in the interference equation (2b), its effect is to scale the slope of equation (3a). Applying the same analysis

$$W_{Ai}/W_{Bi} = Q_i n_i^{-m(K_i/K_{Ai})}/Q_i n_i^{-m(K_i/K_{Bi})} = n_i^{mK_i(1/K_{Bi} - 1/K_{Ai})}$$

Similarly, the same ratio in patch j is

$$W_{Aj}/W_{Bj} = n_j^{mK_j(1/K_{Bj} - 1/K_{Aj})}$$

For the payoff ratios to be equal, so that more than one phenotype can mix across the same two patch types, we therefore require that

$$W_{Ai}/W_{Bi} = W_{Aj}/W_{Bj}$$
$$K_i(1/K_{Bi} - 1/K_{Ai})\log n_i = K_j(1/K_{Bj} - 1/K_{Aj})\log n_j$$

If competitive weights remain constant across patches (the only case so far studied for interference), $K_{Ai} = K_{Aj} = K_A$, $K_{Bi} = K_{Bj} = K_B$, etc. Since we define phenotypes as differing in competitive weights, $K_A \neq K_B$, then

$$K_i \log n_i = K_j \log n_j$$

But from equation (5a) the equilibrium criterion for phenotype A to mix across i, j, is

$$Q_i n_i^{-m(K_i/K_{Ai})} = Q_j n_j^{-m(K_j/K_{Aj})}$$
$$\log Q_i - m(K_i/K_{Ai})\log n_i = \log Q_j - m(K_j/K_{Aj})\log n_j \quad (8)$$

Remembering that $K_i \log n_i = K_j \log n_j$, and that $K_{Ai} = K_{Aj} = K_A$, equilibrium coexistence of more than one phenotype across the same two patch types is impossible in this model unless

$$Q_i = Q_j$$

i.e. unless the patch difference assumption is violated.

In summary, when the effect of competitive differences is felt in scaling the slope of equation (3b) as in the interference model, we cannot have more than one phenotype mixing across the same two patch types. This is a necessary (but not sufficient) condition for the truncated phenotype ESS. We can therefore see why (3a) can lead to multiple mixed strategy equilibria, and why (3b) cannot.

SIMULATIONS

We simulated the two types of model (based on equations 2a, 2b) by assuming that the competitor population consists of 10 phenotypes, each of 20 individuals, in a habitat with 10 patches with values $(Q_i) = 1, 2, \ldots, 10$. The 10 phenotypes had a range of competitive weights = 1, 2, ..., 10. Strategies (choices of patches to exploit) were allowed to replicate in proportion to their payoff, but the numbers of individuals of each phenotype stayed constant throughout the simulation, which was continued until strategy frequencies remained constant. Note that any equilibrium attained will depend on the frequency of the various phenotypes in the population. Our choice of 10 phenotypes, each of 20 individuals, was entirely arbitrary. The value of m was set throughout as 0·5, whether the competitive differences scaled Q_i or m, so as to allow direct comparison.

Figure 2 shows that if phenotypes differ in their intercept (as in equation 3a), then more than one phenotype may straddle the same pair of sites. Thus, in Fig. 2a, all of the phenotypes occur in all of the sites. This is as predicted by the algebraic model.

The distribution of the different phenotypes depends upon the starting conditions. Each simulation for either Fig. 2a, b or c started with a different distribution of individuals between sites. In Fig. 2a the simulation starts with equal numbers of each phenotype in each site. In the simulations for Figs 2b and 2c the initial densities were 1000 times

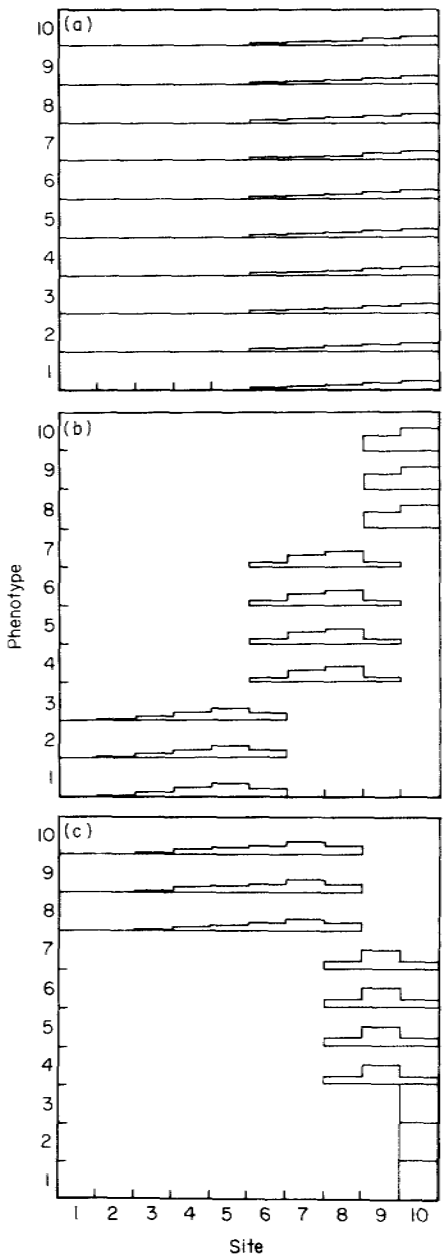


Figure 2. Distribution amongst patches of the 10 different phenotypes in the simulation study, where the phenotype affects the intercept, as modelled in equations (2a) and (3a). Resource quality increases linearly with habitat number. Competitive ability increases linearly with phenotype number. Three different starting conditions are shown: (a) equal numbers in each habitat; (b) phenotypes with highest competitive ability start in the better habitats; and (c) phenotypes with highest competitive ability start in the poorer habitats. See text for further details.

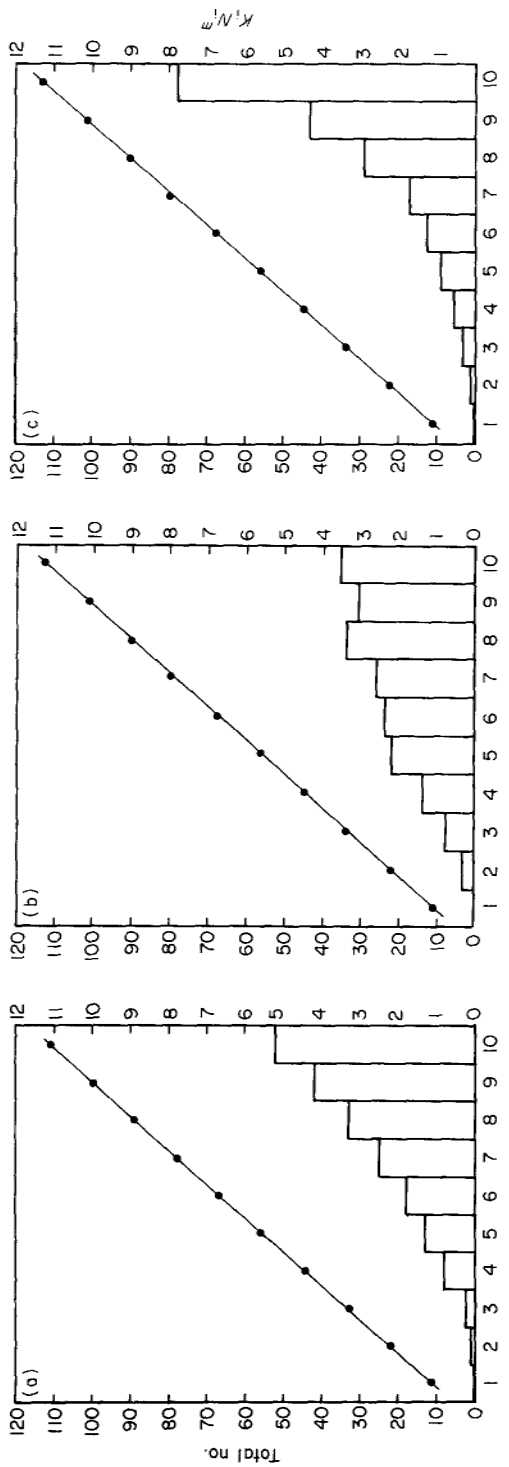


Figure 3. The total number of individuals in each site resulting from the simulations shown in Fig. 2. In (a) there is an equal distribution in each site, in (b) the individuals of high competitive ability are in the richer sites, and in (c) the individuals of high competitive ability are in the poorer sites. ●: value of $K_i n_i^m$ for each site.

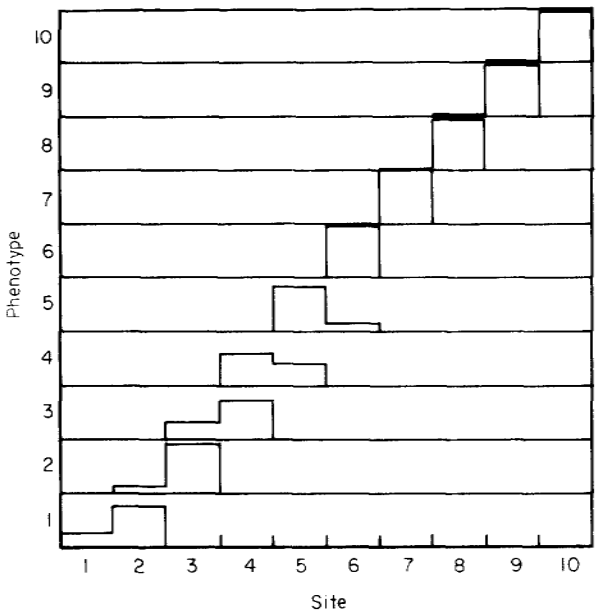


Figure 4. Distribution amongst patches of the 10 different phenotypes in the simulation study, as in Fig. 2 only with phenotype affecting slope, as modelled in equations (2b) and (3b). This distribution was achieved whatever the starting condition.

higher in selected sites than in others. Note that though the total number of each phenotype was held at 20, the number of each phenotype per patch was allowed to take on non-integer values so as to be able to satisfy the equilibrium conditions. For Fig. 2b the initial distribution was adjusted so that the three phenotypes with highest competitive weight started in the best habitats and the three phenotypes with the lowest competitive ability started in the worst habitats. For Fig. 2c this was reversed (individuals with highest competitive ability in the worst sites). In all cases shown in Fig. 2, for each phenotype the intake was equal across sites and running the simulations for further generations (10 000 instead of 200) resulted in no change. This confirms that the distribution is an equilibrium. Although the equilibrium distribution attained depended on the starting conditions, each equilibrium followed rule (7): input rate was balanced by $K_i n_i^m$ for all patches, i. Figure 3 shows the linear relationship between $K_i n_i^m$ and site quality for each of the simulations. The slope of the line varies slightly between simulations (1·117 for Fig. 3a, 1·132 for 3b, and 1·131 for 3c); we are as yet uncertain as to why this should be so.

The eventual number of individuals occurring in each site is dependent upon the initial distribution of phenotypes. Figure 3 shows the numerical response (Holling 1959) for the simulations shown in Fig. 2. There is greater aggregation when individuals with low competitive weight occur in the richer sites (Fig. 3c) than when individuals of high competitive weight occur there (Fig. 3b).

Figure 4 shows the outcome of these simulations when the same set of individual differences in competitive ability affected the slope of log intake in the presence of competition (as in equation 3b; see Fig. 1b). In all simulations we obtained only the truncated phenotype distribution with individuals ranked across sites such that competitive weight correlates with patch quality (the most competitive individuals occupy the best sites). As expected, no more than one phenotype mixed across the same pair of patch types. Unlike the previous model in which the phenotype alters intercepts (Fig. 2), in this model the final distribution was independent of the initial distribution of phenotypes. The starting conditions used to produce Figs 2a, b and c were used and each resulted in the equilibrium shown in Fig. 4. These outcomes from the simulations support those of the algebraic model described earlier. The aggregative numerical response is thus consistent for a given value of m and a range of competitive abilities.

BIOLOGICAL APPLICATION OF THE MODELS

This paper shows that, for equal competitors, there is no obvious theoretical reason why studies of continuous input should give a different response from those of interference; the difference concerns only the range of m (equations 1a, 1b). However, in a review of the literature we (Parker & Sutherland 1986) showed that in empirical studies, phenotypes tended to be distributed equally amongst patches in cases of continuous input, but tended to be distributed unequally in cases of interference.

A plausbile explanation for this relates to the two explicit ways we have chosen to model competitive differences (equations 2a, 2b). In interference studies it seems that the decline in intake rate with the increase in competitors is usually due to differences in aggression, often related to differences in age, sex and dominance, so that different individuals experience different degrees of interference with increased competitor density. This is the case where phenotype scales slope in equation (3b), and which leads to aggregation of the best competitors in the best patches. This model thus seems not only to describe the manner in which interference operates in field studies such as those of oystercatchers, *Haematopus ostralegus* (Goss-Custard et al. 1982, 1984) and herring gulls, *Larus argentatus* (Monaghan 1982), but also to explain the resulting distributions.

In continuous input studies, for example in which birds or fish compete for continually arriving food items, it is likely that relative swimming speed or relative speed of detection of prey can result in differences in intercept between phenotypes. The 'phenotype scales intercept' model of equation (3a) thus seems appropriate and predicts no consistent relationship between phenotype and site quality. Studies of foraging goldfish, *Carassius auratus* (Sutherland et al. 1988) showed that there was no correlation between competitive rank and the time spent in the better site. This also explains why in continuous input studies the average intake rate tends to be the same in all sites (Parker & Sutherland 1986).

Although we suggest it is likely that in interference studies the slope model will often be more appropriate, whereas in continuous input studies the intercept model will be more appropriate, we can think of occasions which may not be that simple. In certain continuous input cases there may be fighting such that some individuals obtain disproportionately little at high densities. An interference model may, at least in part, then be more appropriate. It may then be necessary to consider how phenotype affects both slope and intercept.

Differences in distribution of phenotypes between sites may also be dependent upon a variety of other effects, e.g. perceptual constraints (Abrahams 1986), sampling consequences in small populations (Houston & Macnamara 1988), costs of travel between patches (Korona 1990), differential reinforcement of the competitors (Regelman 1984; see also Milinski & Parker 1991) and variation in predation risk (McNamara & Houston 1990), temporal variability in prey availability (McNamara & Houston 1990) or the conditions under which dominant individuals can defend feeding sites (Inman 1990).

The intercept model applies only to those cases in which the intercept depends upon relative competitive ability. There are other cases in which phenotypes may show consistent absolute differences, which do not vary according to the presence of competitors. For example, oystercatchers may show consistent differences in intercept which are dependent upon differences in foraging ability. Such consistent differences will not affect the distribution.

Extending the intercept model with continuous input and $m=1$, Korona (1989) used a rather different model of competition. As in our models, patches contain competitors varying in competitive weights, but they compete in randomly drawn pairs over each resource item. The probability of success of each is equal to its competitive weight divided by the sum of the two competitive weights. For this form of competition, there is a unique ESS: each patch should contain the same proportions of phenotypes as are found in the entire habitat. Korona's model offers an interesting and plausible explanation of the typical result found in continuous input studies.

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