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Multiple ideal free distributions of unequal competitors

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ABSTRACT

We studied 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 and Grand, 1998) lead to this distribution of equilibria collapsing to a single point. In fact, it can induce the population to shift periodically between equilibria, thereby increasing spatio-temporal variation in competitor numbers. Furthermore, we show that the probability of the system reaching a given equilibrium is critically dependent on the fine detail of the rules describing individual movements.

Keywords: habitat selection, ideal free distribution, patch switching, unequal competitors.

INTRODUCTION

Ideal free distribution (IFD) theory describes how animals should be distributed between a number of resources such than 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 and McNamara, 1988; Milinski and 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 maximizing resource acquisition rate has a profound effect on such systems, such than 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) used 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 in Hugie and Grand, 1998) use fewer (normally considerably

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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.

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 0 and 1 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 which 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; and (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 at random.

MODEL PREDICTIONS

Consider the case where we use 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 Fig. 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

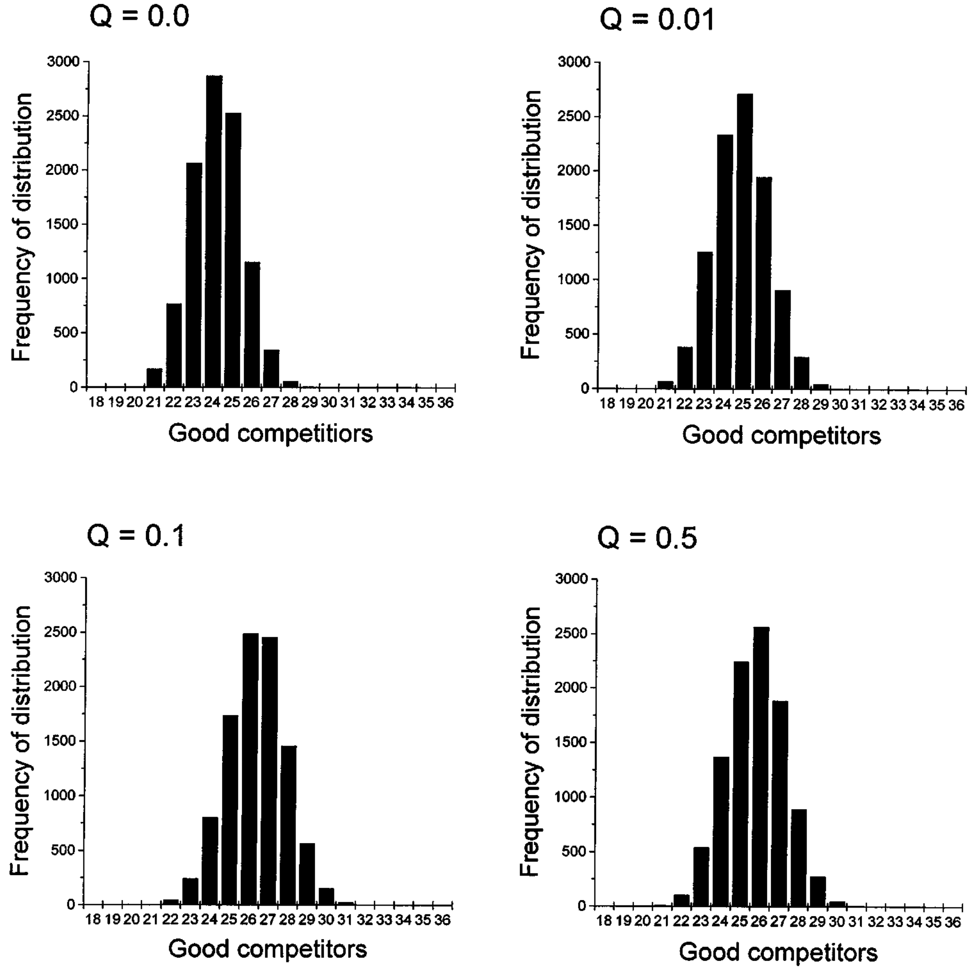

Fig. 1. The model was run with a random selection of IFD movers (case i) for 10,000 simulations, each differing only in the sequence of random numbers used. In each simulation, the number of good competitors in the good patch after 10,000 turns was recorded. The distribution of these numbers is shown 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 and Grand (1998).

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 Fig. 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

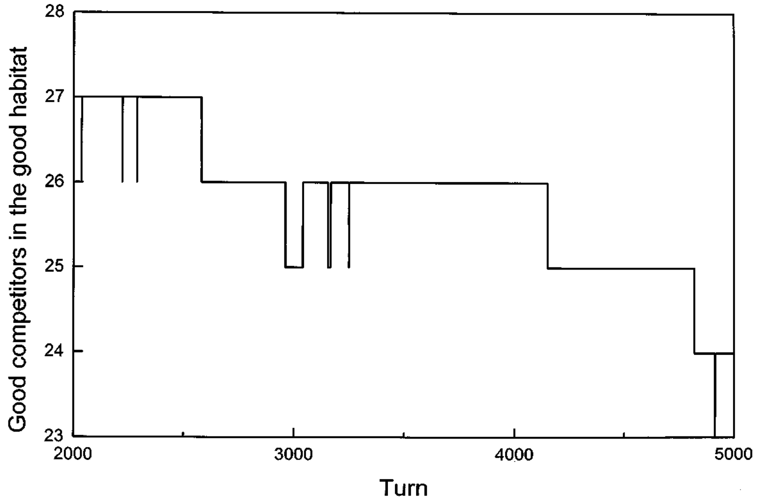

Fig. 2. Time-series showing the number of good individuals in the good patch for part of one simulation with movement case i and $Q = 0.01$. Although the system can spend long periods sitting at an equilibrium, occasionally non-IFD movements produce shifts between equilibria.

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 equilibria is increased, and so the system spends more time away from the equilibria. Furthermore, as Fig. 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 (Figs 1 and 3).

DISCUSSION

The results of 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. Furthermore, 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 which 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, their 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

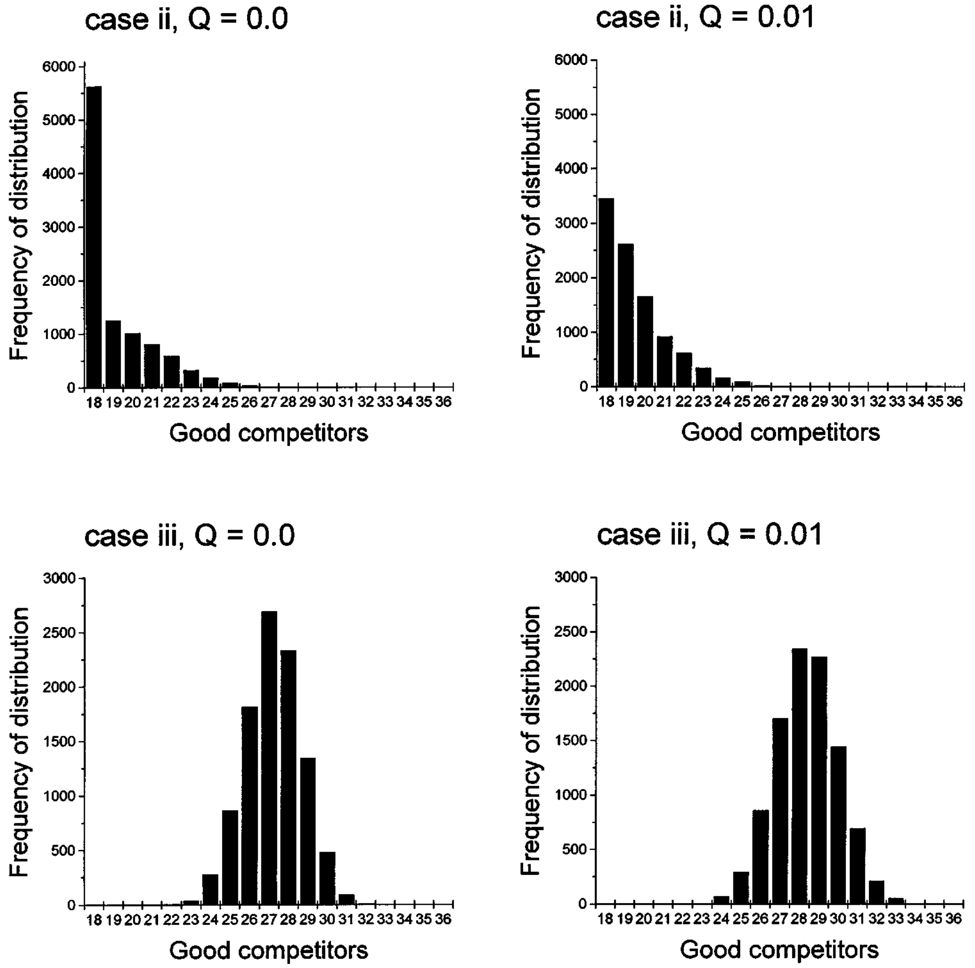

Fig. 3. The model was run for four sets of 10,000 simulations. In each simulation, the number of good competitors in the good patch after 10,000 turns was recorded. The distribution of these numbers is shown for four situations: movement case ii, $Q = 0$; movement case ii, $Q = 0.01$; movement case iii, $Q = 0$; and movement case iii, $Q = 0.01$. In each case, we see considerable variation between simulations, and a strong effect of movement rule.

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 a risk of predation or mating opportunities). We have shown here that non-IFD movements may have profound ecological importance. As Fig. 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 which 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. Furthermore, this effect may be pronounced even when non-IFD movements are rare.

Lastly, a comparison of Figs 1 and 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 and Lang (1998).

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