

Hamilton's rule confronts ideal free habitat selection

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If individuals occupy habitats in a way that maximizes their fitness, if they are free to occupy the habitats they choose and if fitness declines with population density, then their abundance across habitats should follow an ideal free distribution. But, if individuals are genetically related, this simple fitness-maximization mechanism breaks down. Habitat occupation should obey Hamilton's rule (natural selection favours traits causing a loss in individual fitness as long as they result in an equal or greater gain in inclusive fitness) and depends more on inclusive fitness than it does on individual fitness. We demonstrate that the resulting inclusive-fitness distribution inflates the population density in habitats of poorer inherent quality, creating pronounced source-sink dynamics. We also show that density-dependent habitat selection among relatives reinforces behaviours such as group defence and interspecific territoriality, and that it explains many anomalies in dispersal and foraging.

Keywords: evolutionarily stable strategy; evolution; habitat selection; Hamilton's rule; ideal free distribution; inclusive fitness

1. INTRODUCTION

Ideal free theory (Fretwell & Lucas 1970; Fretwell 1972) dominates much of the broad field of behavioural ecology, at least in part because it appears to define the null model for behaviour. Individuals, free of the constraints of social interaction, should distribute themselves among habitats such that each one shares equal expectations of fitness. Since no individual can improve its fitness by moving to another habitat, the ideal free distribution (IFD) is generally thought to represent an evolutionarily stable strategy (ESS) (Maynard Smith 1982; Milinski & Parker 1991). However, among relatives there is no free choice. Selfish decisions are sub-optimal to those that maximize inclusive fitness (Hamilton 1964; Brown 1998). Individuals maximizing inclusive fitness may thus distribute themselves so as to overexploit habitats where each individual has little negative effect on fitness (low fitness loss) while their relatives underexploit habitats where each individual has a large effect (high fitness gain). We extend the IFD theory to explore the consequences of habitat selection in populations of related individuals across two habitats of different quality.

2. AN INCLUSIVE THEORY OF HABITAT SELECTION

We begin by assuming, in habitats 1 and 2, that the total per capita population growth is a function of population size. We now let all individuals be identically related to one another. The inclusive fitness of an individual occupying either habitat 1 or habitat 2 is given by

$$\begin{aligned} I_1 &= f_1(N_1) + r(N_1 - 1)f_1(N_1) + rN_2f_2(N_2) \\ I_2 &= f_2(N_2) + r(N_2 - 1)f_2(N_2) + rN_1f_1(N_1), \end{aligned} \quad (1)$$

respectively, where I represents inclusive fitness, $f_i(N_i)$ is the density-dependent fitness function in habitat i and r is

the coefficient of relatedness. We wish to evaluate when an individual should depart one habitat to live in the other. Assuming negligible cost, the appropriate decision functions to move from habitat 1 to habitat 2 and vice versa are

$$\begin{aligned} B_1 &= I_2(N_1 - 1, N_2 + 1) - I_1(N_1, N_2) \\ B_2 &= I_1(N_1 + 1, N_2 - 1) - I_2(N_1, N_2), \end{aligned} \quad (2)$$

where the first right-hand term is the inclusive fitness of the individual if it moves and the second term is its inclusive fitness if it stays (equation (1)). An individual should move from habitat i whenever $B_i > 0$. For an individual in habitat 1 the decision function can be approximated by

$$B_1 = I_2 - I_1 - \frac{\partial I_2}{\partial N_1} + \frac{\partial I_2}{\partial N_2}, \quad (3)$$

which after substitution from equation (1) becomes

$$\begin{aligned} B_1 &= f_2(N_2) - f_1(N_1) + r(N_2f_2'(N_2) - N_1f_1'(N_1)) \\ &\quad + (1 - r)f_2'(N_2), \end{aligned} \quad (4)$$

where $N_i f_i'$ is the change in fitness in a habitat with changes in population size. The final term will be very small in relation to the others and, for any reasonable value of N_i will be a small fraction of fitness. We define $g(N_1, N_2)$ to represent the remaining terms:

$$g(N_1, N_2) = f_2(N_2) - f_1(N_1) + r(N_2f_2'(N_2) - N_1f_1'(N_1)). \quad (5)$$

After performing the same procedure for B_2 , the decision rules for an individual to migrate can be expressed as $g(N_1, N_2) > 0$ in habitat 1 and $g(N_1, N_2) < 0$ in habitat 2. Note that if all individuals are unrelated ($r=0$) then these conditions reduce to a comparison between f_1 and f_2 such that if $f_1 = f_2$ then there should be no migration, i.e. we have recovered the classic IFD.

To visualize the importance of this result, we let, for the purposes of the argument, the fitness of an individual decline linearly with increasing density in habitat i :

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$$f_i = a_i - b_i N_i, \quad (6)$$

where a_i is the maximum fitness at low density and b_i is the reduction in fitness with density (we provide the general solution to the habitat-selection process under Hamilton's rule for any set of fitness functions in Appendix A). For an IFD, $f_1 = f_2$, and solving for N_2 in the linear model

$$N_2 = \frac{a_2 - a_1}{b_2} + \frac{b_1}{b_2} N_1 \quad (7)$$

defines the isodar, the set of densities in the two habitats where the expected fitness of an individual is the same in both (Morris 1988). Where the individuals are unrelated, equation (7) specifies the condition in which fitness and per capita growth rate are identical in both habitats (because per capita growth rate is the unambiguous fitness definition in this case). For a population of unrelated individuals, there is also no net migration between habitats along the isodar.

If $r > 0$ then equation (7) still holds true for the per capita population growth rate but not for fitness. In this case, the condition for no migration is satisfied when $g = 0$. Substituting equation (6) into equation (5) yields the 'zero-migration' isodar:

$$N_2 = \frac{a_2 - a_1}{b_2(1+r)} + \frac{b_1}{b_2} N_1. \quad (8)$$

Hence, the equal per capita growth-rate isodar (equation (7)) does not coincide with the zero-migration isodar (equation (8)) if the individuals in the population are related ($r > 0$) (figure 1). It is instructive, in the case of related individuals, to determine the combinations of densities in the two habitats that yield no net population growth, i.e. $N_1 f_1 + N_2 f_2 = 0$. In our linear example the resulting zero-total-growth isodar is

$$N_2 = \frac{a_2}{2b_2} + \sqrt{\left(\frac{a_2}{2b_2}\right)^2 + N_1(a_1 - b_1 N_1)}. \quad (9)$$

This arched curve intersects the N_2 -axis (figure 1) at that habitat's equilibrium density, $N_2^* = a_2/b_2$, it intersects the per capita growth-rate isodar at the joint population equilibrium in both habitats (a_1/b_1 , a_2/b_2) and it also intersects the zero-migration isodar.

3. IMPLICATIONS

(a) *Evolutionary strategies and source-sink dynamics*

When $r > 0$, each equilibrium occurs at a different combination of densities (figure 1); there is no simple ESS because the system cannot settle on a single pair of habitat densities. If the migration process is fast compared with population growth then the pattern of habitat occupation will move towards the zero-migration isodar. If the reverse is true then the system tends towards the IFD equilibrium. The result, when individuals are related, is that the resources across habitats will be mismatched in relation to the IFD solution. In figure 1, for example, with rapid migration and $r = 0.5$, the density in habitat 1 is *ca.* 10% above the IFD equilibrium while that in habitat 2 is

ca. 12% less than predicted by the IFD. Thus, relatedness among habitat selectors adds to the list of factors contributing to the widespread observations of mismatching in theoretical and empirical studies (Kennedy & Gray 1993; Ranta *et al.* 1999, 2000). Habitat selection among relatives also changes the traditional fitness equalization across habitats to a source-sink system (Pulliam 1988) or, more precisely, a source-pseudosink system (Kennedy & Gray 1993; Watkinson & Sutherland 1995; Palmqvist *et al.* 2001).

The source-sink dynamics created by inclusive habitat selection may play an important role in population persistence, variability and spatial synchrony. Consider the case of an equilibrium population occupying two habitats where an environmental or other event temporarily impedes the migration between them. The short-term dynamics of a population conforming to an IFD will not be affected (population growth rate is zero in both habitats). A population obeying inclusive habitat selection will fluctuate in both space and time as density declines in the habitat exceeding its carrying capacity and increases in the habitat that is below its carrying capacity. The effect of such increased variation on population persistence will depend on the timing and duration of frustrated migration, time lags in population regulation, relatedness, and the current growth rate of the total population.

The source-sink systems created through habitat selection by related individuals are prone to invasion by unrelated immigrants. Immigrants should preferentially pack the better habitat (the source) because it is underused. The residents' solution to this form of 'habitat parasitism' by unrelated immigrants is simple; they should reduce the cost of habitat selection for relatives and increase the cost for non-relatives. Viewed in this light, the mechanisms of habitat selection become intricately intertwined with the evolution and maintenance of social behaviours such as cooperative breeding (Emlen 1991), interspecific territoriality and sex- or age-biased philopatry. The degree to which immigrants are tolerated is likely to depend on the relative qualities of the habitats. A few immigrants can destabilize the inclusive-fitness distribution between similar habitats supporting low densities, whereas a large number are required to do so in large social groups occupying very heterogeneous habitats.

(b) *Examples from nature?*

Nature is replete with potential examples. Warrior and guard castes in social insects fight to gain and maintain access to resources and space (Wilson 1971; Seger 1991). Naked mole rats have insipient body-size castes where large aggressive individuals are involved in colony defence while smaller individuals specialize in food gathering and tunnel maintenance (Honeycutt 1992). Matrilineal prairie-dog coterries compete with one another for territories and inhibit immigration by unrelated juvenile females (Michener 1983). Related female lions aggressively defend their territory against other females (Packer *et al.* 1990). Little is known about the relative habitat qualities for these various examples but enough is known about the theory to suggest that habitat selection among relatives could play a role in their cooperative behaviours.

The inclusive fitness distribution may be especially applicable to modular, or 'centrally planned' (Brown

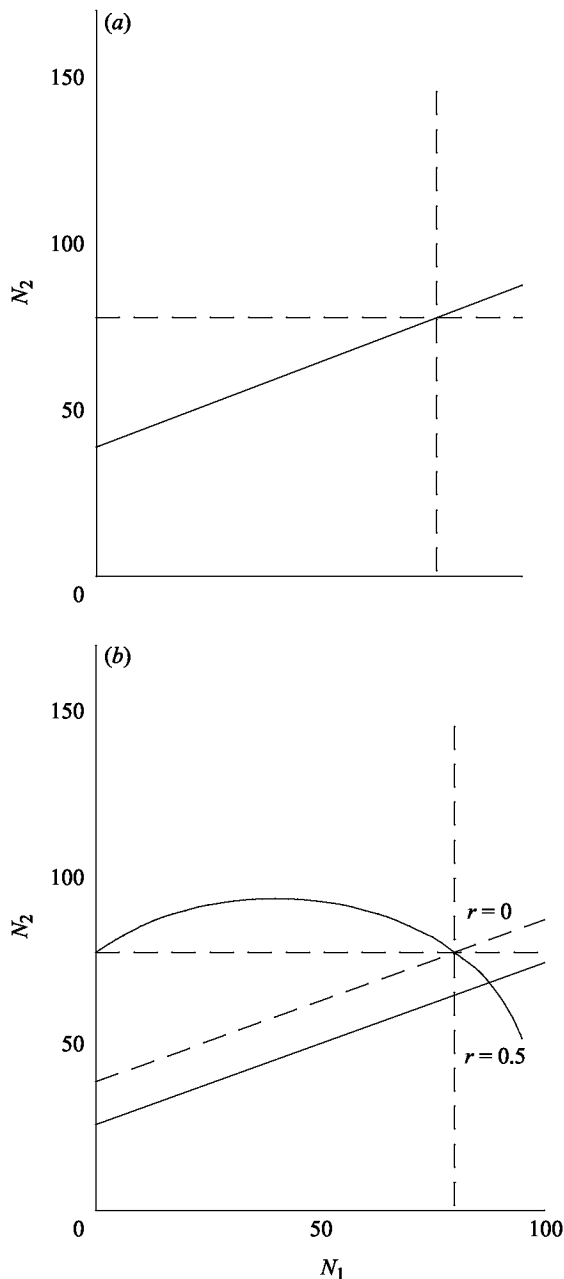


Figure 1. (a) An example of an isodar (solid line) corresponding to ideal free habitat selection when fitness declines linearly with increasing density in habitats 1 and 2. Zero population growth occurs when the density (N) in each habitat is at its respective carrying capacity (a_1/b_1 , vertical dashed line; a_2/b_2 , horizontal dashed line). (b) An example of the inclusive fitness 'no-migration' isodar for the same pair of habitats when individuals are related ($r=0.5$; the IFD isodar ($r=0$, diagonal dashed line) is shown for comparison). An unstable equilibrium occurs at the intersection with the arched zero-total-growth isodar ($N_1=87.65$; $N_2=70.49$). Migration attempts to maintain the equilibrium, which is opposed by positive population growth in habitat 2 and negative population growth in habitat 1 (parameter values correspond to $a_1=80$, $a_2=160$, $b_1=1$, $b_2=2$).

1998), organisms. A plant maximizing mean nutrient uptake might, for example, mismatch its root network to the underlying microhabitat quality. Experiments growing peas in different habitats confirmed that plants

match root biomass to nutrient concentrations and density-dependent competition (Gersani *et al.* 1998). It would be intriguing to repeat these experiments under conditions where the density-dependent uptake rates differ between habitats. We would anticipate not only that the roots would depart from the IFD but also that there might be intense underground physical and chemical contests between the root networks of competing plants. We would also anticipate that modular components in the 'centre' of the organism would more closely approximate an inclusive-fitness distribution than would distal components, which are more easily parasitized by invaders.

Inclusive-fitness distributions should also be common in haplodiploid organisms and the asexual generations of species alternating sexual and parthenogenetic reproduction. In the social Hymenoptera, for example, we would anticipate that single colonies should follow the inclusive-fitness distribution, whereas multiple colonies or species parasitizing one another's habitats should converge on the IFD. We are intrigued, in this respect, by Heinrich's (1976) classical demonstration that multiple species of foraging bumble-bees tend to equalize foraging rewards across different nectar-producing plant species.

Particularly interesting strategies may occur among mutualist species. Imagine the case of a bee-keeper trying to maximize honey production by matching hives with resource patches. The bee-keeper, aiming to achieve equal honey production in all hives, might attempt to allocate them according to the IFD. As long as the hives are not too numerous and as long as each has an independent patch in which its bees can forage, the bees maximize honey production according to the inclusive-fitness distribution, and the bee-keeper's strategy appears brilliant. If the bee-keeper becomes greedy, however, competition among the hives forces the bees into an IFD and production in each hive drops to fit the tragedy of the common resource patches. More convoluted strategies may emerge when both mutualists attempt to attain their respective inclusive-fitness distributions, as might occur in ants tending aphids. As in the bee-keeper example, members of a single clone of aphids might attempt to distribute themselves in order to maximize the resource harvest. Individual ants might then rearrange the aphid distribution to equalize honeydew production. But a colony of ants obeying its own inclusive-fitness distribution might allocate relatively fewer workers to tend aphids in rich patches and relatively more in poor ones. The final strategy in this example depends on the size of the ant colony, the number of aphid clones and whether or not the clones have exclusive access to resource patches.

Inclusive-fitness distributions have important analogues in cultural evolution and economics. Whenever the appropriate fitness currency is density dependent, central planning can maximize total fitness by undermatching density in the richest habitat. As with biological habitat selection, the strategy is easily destabilized by free migration. The recent and historical replacement of centrally planned economies by 'free enterprise' would appear consistent with the prediction.

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APPENDIX A

The inclusive-fitness isodar problem can easily be generalized to any habitat-specific fitness functions. Let f_1 and f_2 be the fitness functions in the two habitats. Letting $f_1 = f_2$ and solving for N_2 as a function of N_1 , we get the classic IFD isodar. Consider a point on the IFD isodar where the system is in dynamic equilibrium (zero population growth in both habitats). Consider now the migration function $g(N_1, N_2)$ (equation (5)), which determines the direction of migration between habitats. Evaluating the migration function at the dynamic equilibrium point, equation (5) simplifies to

$$g(N_1, N_2) = r(N_2 f_2' - N_1 f_1'). \quad (\text{A1})$$

If $g(N_1, N_2)$ is positive then individuals will migrate from habitat 1 to habitat 2; if it is negative then individuals are exported from habitat 2 to habitat 1. In either case, the result is a mismatch between the IFD solution and the actual distribution of individuals between habitats. Hence, the general condition

$$N_2 < \frac{f_1'}{f_2'} N_1 \quad (\text{A2})$$

determines when habitat 1 will be the source (the exporter of individuals) and habitat 2 the (pseudo)sink. The system will settle at an equilibrium if the habitat difference in population growth is outweighed by migration.

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