

Putting competition strategies into ideal free distribution models: Habitat selection as a tug of war

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Abstract

When resources are patchily distributed in an environment, behavioral ecologists frequently turn to ideal free distribution (IFD) models to predict the spatial distribution of organisms. In these models, predictions about distributions depend upon two key factors: the quality of habitat patches and the nature of competition between consumers. Surprisingly, however, no IFD models have explored the possibility that consumers modulate their competitive efforts in an evolutionarily stable manner. Instead, previous models assume that resource acquisition ability and competition are fixed within species or within phenotypes. We explored the consequences of adaptive modulation of competitive effort by incorporating tug-of-war theory into payoff equations from the two main classes of IFD models (continuous input (CI) and interference). In the models we develop, individuals can increase their share of the resources available in a patch, but do so at the costs of increased resource expenditures and increased negative interactions with conspecifics. We show how such models can provide new hypotheses to explain what are thought to be deviations from IFDs (e.g., the frequent observation of fewer animals than predicted in “good” patches of habitat). We also detail straightforward predictions made uniquely by the models we develop, and we outline experimental tests that will distinguish among alternatives.

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1. Introduction

In behavioral ecology, habitat selection is usually modeled as a game against the field (Maynard Smith, 1982): when resources are patchily distributed in the environment, an individual consumer should base its patch-choice decisions not only on the spatial distribution of resources, but also upon the choices of other consumers. This approach to animal spatial distributions was pioneered by Fretwell and Lucas (1970). While they did not phrase their arguments explicitly in terms of game theory and evolutionarily stable strategies (ESSs), the “ideal free distribution” (IFD) (Fretwell and Lucas, 1970) that they predicted as an equilibrium was characterized by the

criterion that, at this distribution, no consumer could increase its resource intake by switching patches. The latter criterion is the essence of a Nash equilibrium (Nash, 1951) or ESS (Maynard Smith and Price, 1973).

Fretwell and Lucas’s (1970) original IFD model contained at least three assumptions (reviewed by Tregenza, 1995) that were considered to be unrealistic for many empirical systems. Consumers were assumed to be: (i) ideal in their knowledge about both the environment and the locations of other conspecifics; (ii) unhindered in traveling to and entering any patch; and (iii) all equal in competitive ability. Thus, myriad extensions followed in which one or more of these assumptions was relaxed (reviewed by Tregenza, 1995). One of the elements common to all these models is that consumers in the same patch negatively impact each other’s payoffs (usually measured in terms of resource intake rates). These negative effects are modeled as arising through a variety of possible mechanisms, such as exploitative competition, general (unspecified) interference, time-wasting interactions, kleptoparasitism, and prey

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suppression (for examples, see Moody and Ruxton, 1996; Parker and Sutherland, 1986; Ruxton and Moody, 1997; Sutherland and Parker, 1985).

Competitive interactions are the heart of intra-specific habitat selection games; if there is no competition, then habitat selection is reduced to a simple optimal foraging problem for an individual whose behavior can be considered in isolation of the behavior of other individuals. With competition included, however, fitness-maximizing patch choices depend critically upon both the locations of other individuals and the precise nature of competition. Accordingly, many IFD models have explored the ways in which different kinds or levels of competition affect predicted distributions (e.g., Humphries et al., 2001; van der Meer and Ens, 1997).

It is therefore surprising that no IFD models have explored the potential consequences of allowing consumers to choose their investments in competition, which might vary in different kinds of patches. Instead, all IFD models to date assume that effort made in acquiring resources (e.g., area of patch explored per unit time) is fixed for a species or for phenotypes within the species. This assumption is rarely mentioned or justified explicitly. Instead, there is little perceived need for justification because of another implicit assumption, namely, that the level of search efficiency or intensity has already evolved to a constrained maximum. The argument for the latter assumption would perhaps be based upon selection for animals to perform maximally within the limits of physical, physiological and energetic constraints. It is certainly true that all animals possess such constraints, but it is far from obvious—and indeed, may be erroneous—that selection will always favor behavior at these limits. For animals that have the potential for frequent interactions (direct or indirect), the assumption of constrained maximum search intensity ignores the existence of a potential tradeoff between the intensity of searching and the extent to which an individual has negative interactions with other consumers. In other words, increasing investment in searching for and acquiring resources may increase the share of resources captured by a consumer but will also increase the costs incurred, and whether costs or benefits accelerate faster will depend upon the number of other consumers present.

Here, we present general, analytic models that extend the fundamental types of IFD models to include ESS patch exploitation behavior that can vary as patch quality or the number of competitors per patch varies. We first present a “continuous input” (CI) (Sutherland and Parker, 1992) patch choice model, in which resources arrive at a fixed rate to each patch and are immediately consumed. We then present an “interference” (Sutherland and Parker, 1992; Tregenza et al., 1996) model that could accommodate various mechanisms of negative interaction between consumers. In order to consider the potential tradeoff between search intensity and negative interactions, we combine familiar IFD payoff structures with tug-of-war theory

(Reeve and Keller, 2001) by assuming that escalating effort by consumers to gain larger shares of available resources ultimately results in a loss of some of those resources.

2. The models

The variables used in the following models are listed in Table 1. All solving, calculus, and simplifications were performed using Mathematica[®] (©Wolfram Research, Inc.).

2.1. Continuous input

Suppose that an environment contains a population of N consumers that must choose between two patches, denoted G and P (G = good, P = poor). In each patch, resources arrive at a fixed rate, v_i ($i = G$ or P), and all resources are used up in each time step. Consider a rare mutant in patch i . Its payoff, W_i , in each time step, given that there are $n_i - 1$ other consumers in i , is

$$W_i = \left(\frac{x_m}{x_m + (n_i - 1)x} \right) v_i (1 - x_m - (n_i - 1)x), \quad (1)$$

where x_m is the mutant's strategy expressed as its effort in acquiring resources and x is the average effort of other individuals in the patch. The first parenthetical expression in Eq. (1) is the mutant's effort relative to the other individuals in the patch. The second parenthetical expression represents the fraction of the resources that remain after the investments in competition are included. Intuitively then, Eq. (1) represents a tradeoff as follows: investing more effort in acquiring resources increases a focal individual's share of the total resources, but decreases the total amount of resources available. To find the ESS level of effort, x^* , in the model represented by Eq. (1), we

Table 1
Definition of variables

Variable	Definition
i	Patch index variable (= “G” for good patch or “P” for poor patch)
v_i	Rate of resource arrival to patch i
n_i	Number of consumers in patch i
N	Total number of consumers in the population
W_i	Individual payoff for choosing patch i
x_m	Effort made by rare mutant in acquiring resources
x	Average effort made by members of population in acquiring resources
x^*	ESS effort level
z	Equilibrium (ESS) proportion of individuals in good patch
a_i	Amount of resources in patch i
s_i	Size (area) of patch i
k	Competition proportionality constant
c	Competition exponent (constant)
R	v_G/v_P or a_G/a_P
m	Coefficient of interference (from traditional interference IFD models)

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