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Ideal Free Distribution in Two Patches*

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Abstract In this survey we discuss some recent progress on the ideal free distribution theory in patch models, with the emphasis on two patches. We show that dispersal strategies leading to the ideal free distributions of organisms are generally evolutionarily stable. We will also study the existence of evolutionarily stable dispersal strategies when dispersal strategies do not lead to the ideal free distributions. Applications to some river models are given.

Keywords Ideal free distribution, population dynamics, competition, patch model, evolutionarily stable strategy.

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1. Introduction

Ideal Free Distribution (abbreviated as IFD henceforth) is a theory for habitat choice of organisms, proposed by Fretwell and Lucas [18]. The basic question is: Given possibly heterogeneous environments, how should organisms distribute themselves in space? Two important assumptions, among others, are stated as follows: First, organisms are aware of the distribution of available resources (ideal); Second, there is no cost of movement (free). Under these assumptions, a prediction of Fretwell and Lucas in their theory is that the distribution of organisms should be proportional to the distribution of resources in space, which is termed as the ideal free distribution. The original statement of Fretwell and Lucas was described in terms of the fitness of organisms. As the ratio of the distribution of organisms versus the distribution of resources can be regarded as the fitness of organisms, in this paper we will refer the ratio of the distributions of organisms and resources as the fitness of the population.

The IFD theory has received tremendous interest in the last few decades, both empirically [35, 39] and theoretically [13, 14, 22, 25, 26]; See the references therein. Many biologists have tried to test this theory through experiments. The first experiment is due to Milinski [35], who used sticklebacks in his experiments. In the experiment, he put 6 fishes in a tank, and allocated one pipe at the left end and another at the right end of the fish tank, respectively, to deliver the food. The ratio of the input rate of the pipes at two ends is 5:1, indicating that the resource distributions at two ends are different. The experimental results show that the ratio of the fishes at two ends is also 5:1, which concurs with the prediction from the ideal free distribution theory. In this experiment, each fish can find out the distribution of the resources by swimming between the two ends of the fish tank, so the fishes

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have "ideal" knowledge of the resources. Since the fish tank is relatively small, the swimming will not cause significant energy loss for fishes, so the movement can be regarded as relatively "free". In the experiment, Milinski also changed the input rates of the pipes at two ends, and he found that the proportions of the fishes at two ends evolved for a period of time, and the new distribution at the equilibrium still adhered to the ideal free distribution.

Evolutionarily stable strategy (ESS) is one of the important objectives in evolutionary biology. A strategy is said to be evolutionarily stable if any population using it can not be invaded by other population, when rare, using a different strategy. One of the topics in the spatial ecology concerns the evolution of dispersal, i.e., to determine dispersal strategies that are evolutionarily stable. In general, strategies that achieve the ideal free distribution are believed to be evolutionarily stable. Therefore, if one can observe that a species achieves an ideal free distribution across the habitat, it is usually equivalent to discovering an evolutionarily stable dispersal strategy which leads to such ideal free distribution. Of course, most of evolutionarily stable dispersal strategies do not necessarily lead to ideal free distributions.

The goal of this paper is to focus on continuous-time and discrete-space models (patch models) for ideal free distribution and to introduce the relevant theory to readers. We mainly aim to discuss some recent progress in the modeling and analysis of patch models for IFD, with the emphasis on two-patch models. We will propose some open questions for interested researchers. There are a vast of literature on ideal free distributions: For further references, we refer to [5, 6] for multi-patch models, [15, 31] for travels with loss, [7, 24] for discrete-time and discrete-space models, [4, 12] for nonlocal movement models, and [1, 3, 8–11, 19, 27, 30] for PDE models.

This paper is organized as follows: In Sect. 2 we discuss the ideal free distribution in a two-patch model with different carrying capacities. Sect. 3 is an application of the main results from Sect. 2 to a two-species river model. In Sect. 4 we consider river model with other boundary conditions and the main focus is the zero Dirichet boundary conditions. In Sect. 5 we extend some results from Sect. 2 for two patches to n patches. In Sect. 6 we discuss relevant questions in spatially and temporally varying environment.

2. Ideal free distribution and balanced dispersal

To study the evolution of dispersal, McPeek and Holt [34] considered a two-patch model which is discrete in both time and space. To present their idea more transparently, we consider a two-patch model:

$$\begin{cases} \frac{du_1}{dt} = d_{12}u_2 - d_{21}u_1 + u_1(1 - \frac{u_1}{K_1}), \quad t > 0, \\ \frac{du_2}{dt} = d_{21}u_1 - d_{12}u_2 + u_2(1 - \frac{u_2}{K_2}), \quad t > 0, \\ u_1(0) > 0, \quad u_2(0) > 0, \end{cases} \tag{2.1}$$

where $u_i(t)$ denotes the number of individuals in patch i, K_i is the carrying capacity of patch i and is assumed to be a positive constant, $i = 1, 2$. d_{12} is the rate of movement from patch 2 to 1, and d_{21} denotes the rate of movement from patch 1 to patch 2. We also assume that d_{12}, d_{21} are positive constants.

As system (2.1) is monotone and sublinear, one can show that (2.1) has a unique